A mathematical model for the control of *Eldana saccharina* Walker using the sterile insect technique

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Declaration

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Abstract

Two mathematical models are formulated in this dissertation for the population growth of an *Eldana saccharina* Walker infestation of sugarcane under the influence of partially sterile released insects. The first model describes the population growth of and interaction between normal and sterile *E. saccharina* moths in a temporally variable, but spatially homogeneous environment. The model consists of a deterministic system of difference equations subject to strictly positive initial data. The primary objective of this model is to determine suitable parameters in terms of which the above population growth and interaction may be quantified and according to which *E. saccharina* infestation levels and the associated sugarcane damage may be measured.

The second model describes this growth and interaction under the influence of partially sterile insects which are released in a temporally variable and spatially heterogeneous environment. The model consists of a discretized reaction-diffusion system with variable diffusion coefficients, subject to strictly positive initial data and zero-flux Neumann boundary conditions on a bounded spatial domain. The primary objectives in this case are to establish a model which may be used within an area-wide integrated pest management programme for *E. saccharina* in order to investigate the efficiency of different sterile moth release strategies in various scenarios without having to conduct formal field experiments, and to present guidelines by which release ratios, frequencies and distributions may be estimated that are expected to lead to suppression of the pest.

In addition to the mathematical models formulated, two practical applications of the models are described. The first application is the development of a user-friendly simulation tool for simulating *E. saccharina* infestation under the influence of sterile insect releases over differently shaped spatial domains. This tool provides the reader with a deeper understanding as to what is involved in applying mathematical models, such as the two described in this dissertation, to real-life scenarios. In the second application, an optimal diversification of sugarcane habitats is considered as an option for minimising average *E. saccharina* infestation levels, and as a further consequence, improving the cost-efficiency of sterile insect releases.

Although many special cases of the above model classes have been used to model the sterile insect technique in the past, few of these models describe the technique for Lepidopteran species with more than one life stage and where F1-sterility is relevant. In addition, none of these models consider the technique when fully sterile females and partially sterile males are being released. The models formulated in this dissertation are also the first to describe the technique applied specifically to *E. saccharina*, and to consider the economic viability of applying the technique to this species. Furthermore, very few examples exist of such models which go beyond a theoretical description and analysis towards practical, real-life applications as illustrated in this dissertation.

Uittreksel

Twee wiskundige modelle word in hierdie proefskrif vir die populasiegroei van 'n *Eldana saccharina* Walker infestasie van suikerriet onder die invloed van gedeeltelik steriele, vrygelate insekte daargestel. Die eerste model beskryf die populasiegroei van en -interaksie tussen normale en steriele *E. saccharina* motte in 'n dinamiese, maar ruimtelik-homogene omgewing. Die model is 'n stelsel deterministiese verskilvergelykings onderhewig aan streng positiewe aanvangswaardes. Die primêre doelstelling met hierdie model is om geskikte parameters te bepaal in terme waarvan die bogenoemde groei en interaksie gekwantifiseer kan word, en waarvolgens *E. saccharina* infestasievlakke en die gepaardgaande suikerrietskade gemeet kan word.

Die tweede model beskryf hierdie groei en interaksie onder die invloed van gedeeltelik steriele insekte wat in 'n dinamiese en ruimtelik-heterogene omgewing vrygelaat word. Die model is 'n gediskretiseerde stelsel reaksie-diffusievergelykings met veranderlike diffusiekoëffisiënte onderhewig aan streng positiewe aanvangswaardes en zero-vloei Neumann-randwaardes op 'n begrensde ruimtelike gebied. Die primêre doelstellings in hierdie geval is om 'n model tot stand te bring wat in 'n area-wye, geïntegreerde pesbestrydingsprogram vir *E. saccharina* gebruik kan word om die doeltreffendheid van verskillende steriele motvrylatingstrategieë te bepaal sonder om daadwerklik veldeksperimente uit te voer, en om riglyne daar te stel waarvolgens vrylatingsverhoudings, -frekwensies en -verspreidings bepaal kan word wat na verwagting na 'n onderdrukking van die pes sal lei.

Bykomend tot die wiskundige modelle in hierdie proefskrif, word twee praktiese toepassings van die modelle ook beskryf. In die eerste toepassing word 'n gebruikersvriendelike simulasie hulpmiddel ontwikkel om *E. saccharina* infestasie onder die invloed van steriele insekvrylatings in verskillende ruimtelike gebiede te simuleer. Hierdie toepassing fasiliteer 'n dieper begrip van wat ter sprake is in die toepassing van wiskundige modelle, soos die twee modelle in hierdie tesis, tot werklike scenario's. In die tweede toepassing word 'n optimale diversifisering van suikerriet habitats as 'n opsie vir die vermindering van die gemiddelde *E. saccharina* infestasie vlakke beskou, en gevolglik word die verbetering van die koste-doeltreffendheid van steriele insekvrylatings afgeskat.

Alhoewel verskeie spesiale gevalle van die bogenoemde twee klasse van modelle reeds in die verlede gebruik is om die doeltreffendheid van die steriele-insektegniek te modelleer, beskryf weinig van hierdie modelle die tegniek vir Lepidopteriese spesies met meer as een lewensfase en waar F1-steriliteit ter sprake is. Verder beskryf geen van hierdie modelle die tegniek waar algeheel steriele wyfies en gedeeltelik steriele mannetjies vrygelaat word nie. Die modelle in hierdie tesis is ook die eerste waar die tegniek spesifiek op *E.saccharina* toegepas word, en waar die ekonomiese lewensvatbaarheid van die tegniek vir hierdie spesie oorweeg word. Verder bestaan daar min voorbeelde van soortgelyke modelle wat verder gaan as 'n teoretiese beskrywing en wiskundige ontleding na praktiese, werklike toepassings, soos in hierdie proefskrif geïllustreer.

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Glossary

Biological control The use of parasites, predators and pathogens for the regulation of unwanted animal or plant populations

Carry-over decision Due to South African mills closing between November and March, a decision has to be made with respect to crops planted late in the season — whether to harvest before November or carry the crop over to March when the mills reopen

Chemical control Using a chemical (for example, a herbicide or pesticide) to control an invasive species

Closed mill period Period between November and March when the South African mills are closed

Cohort Component of a population born during a particular period of time and identified by its period of birth so that its characteristics (such as causes of death and numbers still living) can be ascertained as it progresses to successive time and age periods

Density-dependent A factor that influences individuals in a population to a degree that varies in response to how crowded (dense) the population is

Difference equation A recursive definition of a sequence in which each term depends on a subset of the preceding terms

Differential equation An equation that relates the derivatives of a function of one or more variables to one another

Diffusion The movement of molecules from a high concentration to a low concentration without the application of external forces

Host plant A plant species on which an organism (for example, a parasite) depends, usually as a food source

Integrated Pest Management A combination of biological control, varietal resistance, appropriate farming practices and minimised use of chemical pesticides in order to control a pest species

Ionizing radiation Radiation of such high energy that it can remove electrons from a struck atom, leaving positively charged particles behind. High doses of radiation can cause cellular damage

Larva The newly hatched, wingless, often wormlike form of many insects before metamorphosis

Lepidoptera An order of insects, comprising butterflies, moths, and skippers, that as adults have four membranous wings more or less covered with scales

Logistic growth Population growth in which the growth rate decreases with an increasing number of individuals until it becomes zero when the population reaches a maximum

Mean-field assumption The assumption that individual organisms encounter one another in proportion to their average abundance across space

Milling season That part of the year during which sugarcane is processed at mills (from March to November in South Africa)

Node The point on a stem where a leaf is attached

Oviposition The process of laying eggs by oviparous animals through an ovipositor

Parasitoid An organism that lives at the expense of another (its host), impedes its growth and eventually kills it

Polyandrous A mating pattern in which a female mates with more than one male during a single breeding season

Population dynamics The aggregate of processes that determine the size and composition of a population

Pre-trashing The process of removing dry leaves from sugarcane stalks

Pupa An insect in the nonfeeding, usually immobile, transformation stage between the larva and the moth

Ratoon A shoot sprouting from a plant base

Simulation A process (usually implemented on a computer) during which real world systems or processes are emulated or mimiced

Spermatophore A capsule or mass created by males of various animal species, containing spermatozoa and transferred in its entirety to the female's ovipore during copulation

Stalk A stem or main axis of a herbaceous plant

Stalk borer Insect of which the larvae bore into the stalks causing injury to a plant

Sterile Insect Technique A method of biological control whereby many laboratory-reared sterile insects are released into a native population

Sucrose The organic compound commonly known as table sugar and sometimes called saccharose

Validation The process of determining the degree to which a model is an accurate representation of the real world from the perspective of the intended uses of the model

Verification The process of determining whether a model implementation accurately represents the developer's conceptual description of the model and the solution to the model

List of Acronyms

ATV All terrain vehicle

AW-IPM Area-wide integrated pest management

DSS Decision support system

IAEA International Atomic Energy Agency

IPM Integrated pest management

GIS Geographic information system

SASRI South African Sugarcane Research Institute

SIT Sterile insect technique

UAV Unmanned air vehicle

List of Reserved Symbols

The symbols listed below are reserved for a specific use, unless specified otherwise in a localised section where their meanings are apparent. Other symbols may be used throughout the dissertation in an unreserved fashion.

Symbols in this dissertation will conform to the following convention:		
$\mathbf{A}$	Symbol denoting a **matrix**	(Boldface capitals)
$\underline{a}$	Symbol denoting a **vector**	(Underlined lower case letters)

Symbol	Meaning
Functions & formulas	
$\alpha_E(t,\tau)$	Egg maturation rate
$\alpha_{L_1}(t,\tau)$	Larval maturation rate (outside stalk)
$\alpha_{L_2}(t,\tau)$	Larval maturation rate (inside stalk)
$\alpha_P(t,\tau)$	Pupal maturation rate
$b(t)$	Density-dependent mortality rate
$b(\underline{\xi},t)$	Density-dependent mortality rate at position $\underline{\xi}$
C	Total cost of release strategy
$\gamma(t)$	Probability of a fertile egg being fertilized by a fertile sperm
$\gamma(\underline{\xi},t)$	Probability of a fertile egg being fertilized by a fertile sperm at position $\underline{\xi}$
$d(\underline{\xi})$	Diffusion coefficient at position $\underline{\xi}$
$\delta(t)$	Percentage stalk length bored (damage index)
$\delta(\underline{\xi},t)$	Percentage stalk length bored (damage index) at position $\underline{\xi}$
$f_i(t,\underline{E})$	Number of the i-th population created during one time-step
$f_i(\underline{\xi},t,\underline{E})$	Number of the i-th population created during one time-step at position $\underline{\xi}$
$g_e(\tau)$	Polynomial used to obtain the egg maturation rate at temperature τ
$g_{l_1}(\tau)$	Polynomial used to obtain the larval maturation rate (outside stalk) at temperature τ
$g_{l_2}(\tau)$	Polynomial used to obtain the larval maturation rate (inside stalk) at temperature τ
$g_p(\tau)$	Polynomial used to obtain the pupal maturation rate at temperature τ
I	Increase in revenue as a result of SIT
$k_e(\tau)$	Polynomial used to obtain the egg mortality rate at temperature τ
$k_l(\tau)$	Polynomial used to obtain the larval mortality rate at temperature τ
$k_p(\tau)$	Polynomial used to obtain the pupal mortality rate at temperature τ
$k_m(\tau)$	Polynomial used to obtain the moth mortality rate at temperature τ

$\ell(t)$	Average stalk length on day t
$\rho(t)$	Probability of a fertile egg being fertilized by a semi-sterile sperm
$\rho(\underline{\xi}, t)$	Probability of a fertile egg being fertilized by a semi-sterile sperm at position $\underline{\xi}$
$r(t)$	Release rate of sterile moths
$r(\underline{\xi}, t)$	Release rate of sterile moths at position $\underline{\xi}$
RV	Recoverable value
S	Percentage sucrose in cane delivered
$\mu_E(t, \tau)$	Egg mortality rate
$\mu_{L_1}(t, \tau)$	Larval mortality rate (outside stalk)
$\mu_{L_2}(t, \tau)$	Larval mortality rate (inside stalk)
$\mu_{L_1}(\underline{\xi}, t, \tau)$	Larval mortality rate (outside stalk) at position $\underline{\xi}$
$\mu_{L_2}(\underline{\xi}, t, \tau)$	Larval mortality rate (inside stalk) at position $\underline{\xi}$
$\mu_P(t, \tau)$	Pupal mortality rate
$\mu_M(t, \tau)$	Moth mortality rate
$\mu_S(t, \tau)$	Radiated moth mortality rate
$v(\omega)$	Function which adjusts the larval mortality rate according to the resistance rating ω of the cane variety
$P_{ff}(t)$	Probability of mating with a fertile female
$P_{if}(t)$	Probability of mating with an inherited sterile female
$P_{rf}(t)$	Probability of mating with a released sterile female
$P_{fm}(t)$	Probability of mating with a fertile male
$P_{im}(t)$	Probability of mating with an inherited sterile male
$P_{rm}(t)$	Probability of mating with a released male
$P_{ff}(\underline{\xi}, t)$	Probability of mating with a fertile female at position $\underline{\xi}$
$P_{if}(\underline{\xi}, t)$	Probability of mating with an inherited sterile female at position $\underline{\xi}$
$P_{rf}(\underline{\xi}, t)$	Probability of mating with a released sterile female at position $\underline{\xi}$
$P_{fm}(\underline{\xi}, t)$	Probability of mating with a fertile male at position $\underline{\xi}$
$P_{im}(\underline{\xi}, t)$	Probability of mating with an inherited sterile male at position $\underline{\xi}$
$P_{rm}(\underline{\xi}, t)$	Probability of mating with a released male at position $\underline{\xi}$
$\sigma(t, \tau)$	Amount of larval feeding
T	Average number of tons of sugarcane delivered
$T(\underline{\xi})$	Average number of tons of sugarcane delivered at position $\underline{\xi}$
W	Revenue (payment due to a farmer for cane delivered)
W_{SIT}	Revenue (payment due to a farmer for cane delivered) if an SIT strategy is applied
Sets	
$\mathcal{S}$	2-dimensional spatial domain
Parameters	
a	Age of sugarcane in days
A	Maximum number of matings possible per female
B	Maximum number of matings possible per male
β	Fertile fraction of eggs from the F_1 progeny of released males
c_m	Competivity of released sterile males in relation to wild males
c_f	Competivity of released sterile females in relation to wild females
c_s	Competivity of the sperm of released sterile moths in relation to the sperm of wild moths

F	Percentage of fibre in cane delivered
F_n	Proportion of females mating n times
h	Number of hectares of field
h_p	Number of hectares of habitat patch
κ_r	Cost of raising and sterilising one *E.saccharina* moth
κ_l	Labour cost per hectare for releasing sterile moths
κ_f	Fuel cost per hectare for transporting sterile moths on the release site
m	Male proportion of released sterile moths
M_n	Proportion of males mating n times
N	Percentage of non-sucrose in cane delivered
q	Proportion of released moths which escaped radiation and are therefore fertile
λ_f	Egg laying rate of a fertile female mated with a fertile male
λ_s	Egg laying rate of a fertile female mated with a released sterile male
y	Density-dependent function parameter
z	Density-dependent function parameter
Variables	
$\mathbf{D}$	Diffusion coefficient matrix
$E_1(t)$	Population density of fertile egg population
$E_2(t)$	Population density of inherited sterile egg population
$E_3(t)$	Population density of fertile larval population (outside stalk)
$E_4(t)$	Population density of inherited sterile larval population (outside stalk)
$E_5(t)$	Population density of fertile larval population (inside stalk)
$E_6(t)$	Population density of inherited sterile larval population (inside stalk)
$E_7(t)$	Population density of fertile pupal population
$E_8(t)$	Population density of inherited sterile pupal population
$E_9(t)$	Population density of fertile moth population
$E_{10}(t)$	Population density of inherited sterile moth population
$E_{11}(t)$	Population density of released sterile moth population
$\mathcal{E}_1(t)$	Non-dimensional population density of fertile egg population
$\mathcal{E}_2(t)$	Non-dimensional population density of inherited sterile egg population
$\mathcal{E}_3(t)$	Non-dimensional population density of fertile larval population (outside stalk)
$\mathcal{E}_4(t)$	Non-dimensional population density of inherited sterile larval population (outside stalk)
$\mathcal{E}_5(t)$	Non-dimensional population density of fertile larval population (inside stalk)
$\mathcal{E}_6(t)$	Non-dimensional population density of inherited sterile larval population (inside stalk)
$\mathcal{E}_7(t)$	Non-dimensional population density of fertile pupal population
$\mathcal{E}_8(t)$	Non-dimensional population density of inherited sterile pupal population
$\mathcal{E}_9(t)$	Non-dimensional population density of fertile moth population
$\mathcal{E}_{10}(t)$	Non-dimensional population density of inherited sterile moth population
$\mathcal{E}_{11}(t)$	Non-dimensional population density of released sterile moth population
$E_1(\underline{\xi}, t)$	Population density of fertile egg population at position $\underline{\xi}$
$E_2(\underline{\xi}, t)$	Population density of inherited sterile egg population at position $\underline{\xi}$
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$\mathcal{E}_5(\underline{\xi}, t)$	Non-dimensional population density of fertile larval population (inside stalk) at position $\underline{\xi}$
$\mathcal{E}_6(\underline{\xi}, t)$	Non-dimensional population density of inherited sterile larval population (inside stalk) at position $\underline{\xi}$
$\mathcal{E}_7(\underline{\xi}, t)$	Non-dimensional population density of fertile pupal population at position $\underline{\xi}$
$\mathcal{E}_8(\underline{\xi}, t)$	Non-dimensional population density of inherited sterile pupal population at position $\underline{\xi}$
$\mathcal{E}_9(\underline{\xi}, t)$	Non-dimensional population density of fertile moth population at position $\underline{\xi}$
$\mathcal{E}_{10}(\underline{\xi}, t)$	Non-dimensional population density of inherited sterile moth population at position $\underline{\xi}$
$\mathcal{E}_{11}(\underline{\xi}, t)$	Non-dimensional population density of released sterile moth population at position $\underline{\xi}$
$\underline{\xi}$	Position vector in spatial domain
t	Time (in days)
τ	Temperature
ω	Resistance rating
$\underline{x}$	Non-dimensional position vector

CHAPTER 1

Introduction

Contents

"For, usually and fitly, the presence of an introduction is held to imply that there is something of consequence and importance to be introduced."

— Arthur Machen

1.1 Background

The South African sugar industry is recognised as one of the top fifteen leading cost competitive sugar producers in the world. Its export infrastructure, agricultural and industrial research platforms and efficient industry organisation are considered to be the key drivers of its success. The industry makes an important contribution to employment, sustainable development and the national economy in South Africa with an estimated one million people depending on the sugar industry for a living.

South African sugarcane is produced mainly in the province of KwaZulu-Natal; close to 68 percent of the produce is grown within 30 kilometres of the coast and 17 percent in the KwaZulu-Natal midlands. Other producing areas include Northern Pondoland, the Eastern Cape, Pongola and the Mpumalanga lowveld (see Figure 1.1). Approximately 38 200 registered sugarcane growers farm in KwaZulu-Natal, Mpumalanga and the Eastern Cape, and fourteen sugarmills operate in these regions. An estimated average of 2.3 million tons of sugar are produced per season of which approximately 40% is exported to international markets, including those in Africa, Asia and the Middle East. The industry generates an annual estimated average direct income of R7 billion [98].

A major threat to the industry's profit margins is the African stalk borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae), which has been identified as a serious pest in sugarcane plantations in South Africa since 1971 [25]. Infestation results in serious losses in sucrose production,

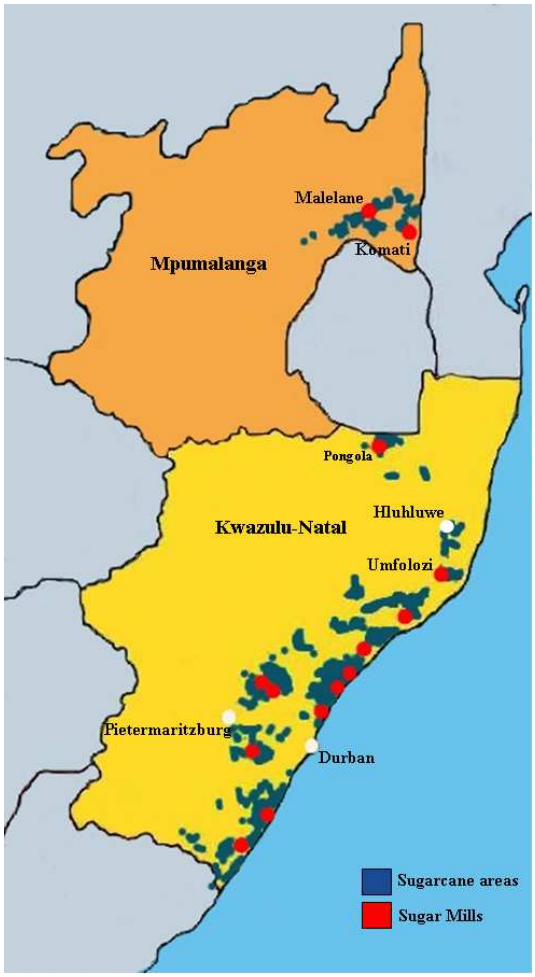


FIGURE 1.1: *Sugar producing areas in South Africa [98].*

not only affecting the sucrose content of sugarcane, but also the final sugarcane biomass. The Eldana problem is thus of major concern among sugarcane farmers in South Africa, and a means of effectively managing the pest is the subject of a number of intensive research programmes at the *South African Sugarcane Research Institute* (SASRI). These research programmes have focussed on chemical control [50], crop management [26, 29, 66, 114], varietal resistance [52, 58], biological control [31, 32, 33, 34] and more recently the *Sterile Insect Technique* (SIT), a birth control method implemented by the release of a large number of sterile insects as part of SASRI's *area-wide integrated pest management program* (AW-IPM).

SIT was initiated in South Africa in 1996 to create fruit fly-free areas in the Western Cape from both the Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae) and the Natal fruit fly *Ceratitis rosa* (Diptera: Tephritidae). An SIT pilot project in the Hex River valley proved successful in terms of control, but the prospect of complete eradication of fruit flies will only be considered when economically justified. In 2003 the *International Atomic Energy Agency* (IAEA) approved funding for an SIT project against the codling moth *Cydia pomonella* (Lepidoptera: Tortricidae), the false codling moth *Thaumatotibia leucotreta* (Lepidoptera: Tortricidae) and the Natal fruit fly [2]. An SIT programme was initiated against false codling moth in the Citrusdal citrus growing region of the Western Cape in 2007. During the 2008/2009 growing season, the native population of false codling moth and the amount of infested fruit declined significantly where releases occurred. This was in contrast with areas where no releases

occurred and infestation remained high [47]. As a result of the similarities between the false codling moth and the eldana moth, the use of SIT against *E. saccharina* was deemed feasible. In 2009 the IAEA approved further funding for an SIT project involving four Lepidoptera pests, one of which is the sugarcane borer *E. saccharina*, under the management of SASRI. To this end a 10-year business plan will be developed with a view to obtain government support for a coordinated SIT programme in South Africa [2]. Two pilot sites near Eston have been identified as areas where the SIT project will be conducted [35].

1.2 Informal Problem Description

A necessary prerequisite for any SIT programme is a proper understanding of the effects of sterilisation through radiation on the physiological and behavioural aspects of the specific insect. Research projects on *E. saccharina* physiology and its behaviour after sterilisation are being conducted at SASRI and at Stellenbosch University. Invaluable insights into the mortality, levels of sterility [110] and competitiveness in matings of the sterile insects [73] for different radiation doses have been gained in these projects. As a result of this information, it is possible to raise large numbers of sterile insects in a laboratory with the necessary traits to be able to survive and mate. These laboratory-reared insects may then be released into native populations.

A successful SIT programme requires either suppression or total eradication of the relevant pest according to an economically viable release strategy. In order to suppress or eradicate a pest, typical SIT questions raised are what the necessary numbers of sterile insects to release are, what the best timing during the year for these releases will be, how frequent releases should be and what the best spatial distribution for release sites will be. An increase in production and income as a result of sterile releases must also be sufficiently large in order to justify the costs involved in such a programme. It is therefore necessary to also consider what the optimal release strategy in terms of cost will be. The purpose of this dissertation is to aid the current South African SIT research effort and to help answer some of the questions mentioned above via the use of mathematical and simulation models for studying the possible effects of artificial SIT interference in native *E. saccharina* populations. From studying biological interaction models it is known that a system can be driven to be unstable if certain parameters are changed appropriately, that is, if their values pass through bifurcation values. Considerable scientific studies should therefore be carried out before any natural system is altered by external manipulation, such as biological pest control or SIT, in order to avoid wasting time, money, effort and possibly altering a system into the least desired ecological outcome [74].

1.3 Scope and Objectives of this Dissertation

The scope of this dissertation shall be restricted to *E. saccharina* infestation and the problems associated with SIT as a control measure, contained within the broader area of integrated pest management in sugarcane, and excludes a detailed mathematical description of sugarcane growth, cultivation, harvesting and control measures other than SIT used in an AW-IPM. The main contribution is the development of a general mathematical model which is able to describe *E. saccharina* population growth, dispersal and interaction with sterile insects in sugarcane in various scenarios and parameter spaces. In order to aid the current SIT effort with respect to *E. saccharina*, the following research objectives are pursued in this dissertation:

Objective I: To *perform a literature survey of E. saccharina growth in sugarcane and SIT* in

general. Such a context should provide the necessary biological background for formulating a realistic mathematical model of *E. saccharina* population growth and interaction with sterile insects in sugarcane.

Objective II: To *perform a literature survey of mathematical models* previously formulated in the context of *E. saccharina* growth in sugarcane, general SIT and dispersal in order to establish a foundation of scientifically sound and suitable models which may be adopted in an appropriately abridged form along with the appropriate solution methods.

Objective III: To *develop and present a general mathematical model* of *E. saccharina* growth and interaction with released sterile insects in sugarcane by

a) *determining suitable parameters* (and their values) for describing *E. saccharina* growth and interaction with released sterile insects;

b) *formulating suitable equations* which capture *E. saccharina* population growth with sterile releases;

c) *determining the contribution* of each of the parameters towards *E. saccharina* population growth and sugarcane damage;

d) *validating* its mathematical content;

Objective IV: To *develop a general spatio-temporal model* of *E. saccharina* growth and dispersal in a heterogeneous sugarcane environment and to present and motivate its mathematical problem formulation.

Objective V: To *estimate*, by means of the models in Objectives III and IV above, the *optimal release method, distribution, frequency and ratio* for which profit is maximised and sugarcane damage is minimised, given a suitable set of parameter values.

Objective VI: To *determine* whether or not SIT is an *economically viable control measure* for *E. saccharina* infestation in sugarcane.

Objective VII: To *develop a user-friendly simulation tool* which may be used to investigate different SIT scenarios — thereby developing a basic framework from which to further advance toward decision support for an AW-IPM.

Objective VIII: To *illustrate how the models in Objectives III and IV above may be applied* to a specific scenario within the sugarcane farming context.

Objective IX: *To provide possible future directions of research* along which to proceed.

1.4 Dissertation Organization

This dissertation comprises eight chapters, including this introductory chapter. Chapter 2 provides the reader with a basic understanding of sugarcane growth in South Africa, *Eldana saccharina* Walker infestation and population growth in sugarcane, as well as the use of SIT. The chapter contains the necessary information for understanding the model assumptions made later during model formulation.

The purpose of Chapter 3 is to provide a review of previous mathematical models formulated to describe *E. saccharina* infestation and population growth in sugarcane. The chapter also

provides examples of other, related SIT models formulated and finally explains the modelling approach adopted in this dissertation.

Chapter 4 contains a detailed description and derivation of the mean-field *E. saccharina* population growth model with sterile releases, as well as the derivation of the growth, maturation, mortality and SIT parameters assumed in this dissertation. Model validation is performed by means of limited data sets obtained from the Sezela mill and the pilot site near Eston. The chapter closes with a presentation of various results from numerical and sensitivity analyses.

The mean-field model of Chapter 4 is extended to a spatio-temporal model in Chapter 5. The chapter includes a derivation of zero-flux Neumann boundary conditions on a discretized spatial domain with variable diffusion coefficients, and an estimation of a suitable range for a constant diffusion coefficient applicable to *E. saccharina* dispersal. Various SIT release methods are considered, along with the resulting distributions of released sterile insects within the spatial domain. The chapter closes with a presentation of numerical results obtained from simulations.

The practical workability of the spatio-temporal model of Chapter 5 within a real-life SIT scenario is demonstrated in Chapter 6. The chapter contains a description of a novel user-friendly simulation tool developed and provides a basic platform from which different release strategies may be investigated with respect to various spatial domains. Results from simulations performed on a domain similar to the field layout of the Eston pilot site are presented.

One possible way of improving the cost-efficiency of SIT is explored in Chapter 7. The chapter contains modelling contributions made towards the suppression of *E. saccharina* in different heterogeneous sugarcane layouts with respect to both sugarcane age and the harvesting of the sugarcane at different points in time. The reaction-diffusion model developed in Chapter 5 is utilised to perform the necessary simulations.

Finally, a short dissertation summary is presented in Chapter 8, together with an overview of the contributions made in this dissertation. Suggestions with respect to future work which may further improve on the work contained in this dissertation are also given.

CHAPTER 2

Survey of biological literature

Contents

"The one and only substitute for experience which we have not ourselves had is literature."
— Alexander Solzhenitsyn

In this chapter a biological background is provided with regards to sugarcane in South Africa, *E. saccharina* infestation and population growth in sugarcane, and the Sterile Insect Technique. The chapter provides the necessary biological foundation to understand the research assumptions made during model construction later in this dissertation.

2.1 Sugarcane

Sugarcane (*Saccharum officinarum L.*) is a tall perennial grass from the family *Gramineae* (see Figure 2.1). The sugarcane stalk consists of sections which vary between 11 and 18 cm in length with each section comprising of a node and an internode (see Figure 2.2). The stalks have a diameter of between 2 and 5 cm and the sugarcane canopy can reach a height of up to 6 metres with long, swordlike green leaves on the upper parts and dead leaves on the lower parts of the stalks. Each node of the stalk contains a bud from which a new plant may emerge. Sugarcane grows best in a tropical climate in fertile and moist soil. During its growth various diseases and pests can damage sugarcane which, in turn, results in yield losses [53, 104].

To ensure the next year's crop, the cane roots are left in the field to regrow for an additional year (a *ratoon*) when the stalks are harvested, or the roots are ploughed out and new mature cane stalks are cut into sections (*setts*) and laid horizontally in furrows and then covered with soil. New plants spring from the buds of these cuttings. Sugarcane farmers usually plant adjacent fields with different varieties suited to local growing conditions. When sugarcane matures, each stool may contain 3–6 mature stalks. The maturation time of sugarcane varies according to the

FIGURE 2.1: *Sugarcane fields in Kwazulu-Natal [73].*

location. In South Africa, the maturation time varies between 12 and 24 months. At the coast, the maturation time is 12–16 months, while the maturation time inland is 22–24 months. In order to maximise sucrose production, it is important that sugarcane is grown long enough to mature. Farmers must manage their cane fields carefully up to harvest in order to maximise their profit over the entire season. Also, as a result of the mills closing between December and March, farmers have the option to keep a portion of sugarcane planted for harvest and milling in the following season in order to have mature sugarcane available for harvesting at the beginning of the new season. Sugarcane left to mature in the closed mill period is known as carry-over cane and is vulnerable to high levels of *E. saccharina* infestation necessitating its early cutting and therefore a loss in potential production. The fields selected for harvesting are burnt just prior to harvesting with harvesting commencing as soon as possible thereafter. The harvested cane is then transported to the nearest mill where it is weighed and tested for quality before being processed for sugar [33, 53, 67, 100].

2.2 *Eldana saccharina* Walker

The stalk borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae) is indigenous to Africa, occurring naturally in wetland sedges and indigenous grasses. It is limited to areas with warm temperatures and relatively high rainfall, and prefers dead leaf material for oviposition [3, 4]. It was first described as a pest in 1865 in the sugarcane fields of Sierra Leone [109] and is probably the only consistently serious insect pest attacking sugarcane in Africa [7]. In South Africa, *E. saccharina* invaded sugarcane in the Umfolozi area from 1939 to 1950, and again in 1970 in the Hluhluwe area, from where it has spread north and south. Since 1970 it has grown to be a serious pest in the sugarcane areas of Kwazulu-Natal, Swaziland and Mpumalanga, with infestation in some areas so serious that it has, at times, caused consignments of sugarcane to be rejected at the mill. It is debatable whether it was the widespread distribution or the widespread destruction of the insect's natural host that has contributed to the spread of the outbreak. This widespread distribution or destruction also appears to have contributed more to

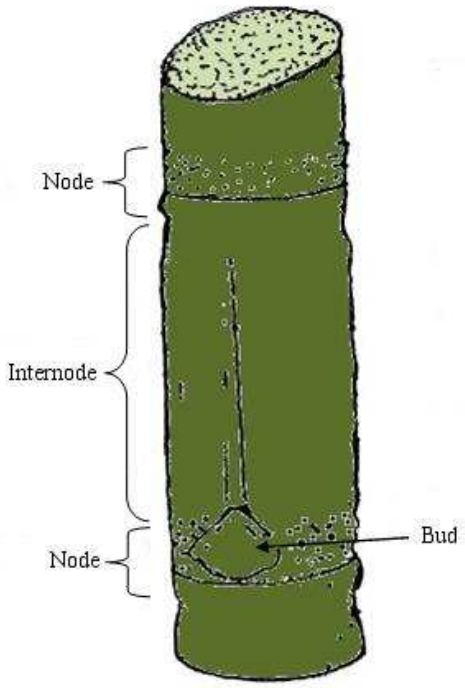


FIGURE 2.2: *Section of a sugarcane stalk [75].*

the outbreak than the use of infested seedcane or migration [8, 25, 35]. Evidence has suggested that *E. saccharina* infestation of sugarcane was originally a result of the attractive egg-laying sites (dead leaf material) rather than sugarcane being a more nutritious host [3]. As a result of an increased use of nitrogen and potassium fertilizers in crop production, the nutritious quality of crops have improved greatly, making them even more attractive [4, 8]. The ability of *E. saccharina* to hide in the new host plants from natural enemies, may have further helped the insect to establish itself on sugarcane [33].

2.2.1 *E. saccharina* on sugarcane

The life cycle of *E. saccharina* is typical of insects, consisting of eggs, larvae, pupae and moths (see Figure 2.3) [4, 7, 25, 52, 90]. The time spent in each stage of the lifecycle is variable, depending as much on the quality of food as on the temperature experienced [7, 52, 111]. On average, however, eggs hatch after 8–10 days, larvae mature after 20 days in summer and after 60 days in winter, and from pupae the moths emerge after ± 10 days [25], with variation in development time between individuals of the same cohort. Moths have a lifespan of 5–7 days. As a result of individual variation in development time, generations completely overlap with all stages in the life cycle present at all times [7].

Adult females lay their eggs on the lower parts of the plant between the trash and dry leaf sheaths [3, 25, 66]. Evidence from laboratory experiments suggests the possibility of density-dependent oviposition and fecundity of females [90]. Larvae hatching from the eggs disperse from the oviposition sites and feed initially on cane leaves and under leaf sheaths on organic matter. When the larvae are sufficiently robust, they start boring into the stalk, normally through the bud or root primordia, and feed on the internal tissues causing yield losses in sugarcane [3, 25]. The presence of frass (feeding waste), appearing on the outside of the stalk, is an indication of borer infestation [90]. Figure 2.4 shows a typical damaged sugarcane stalk

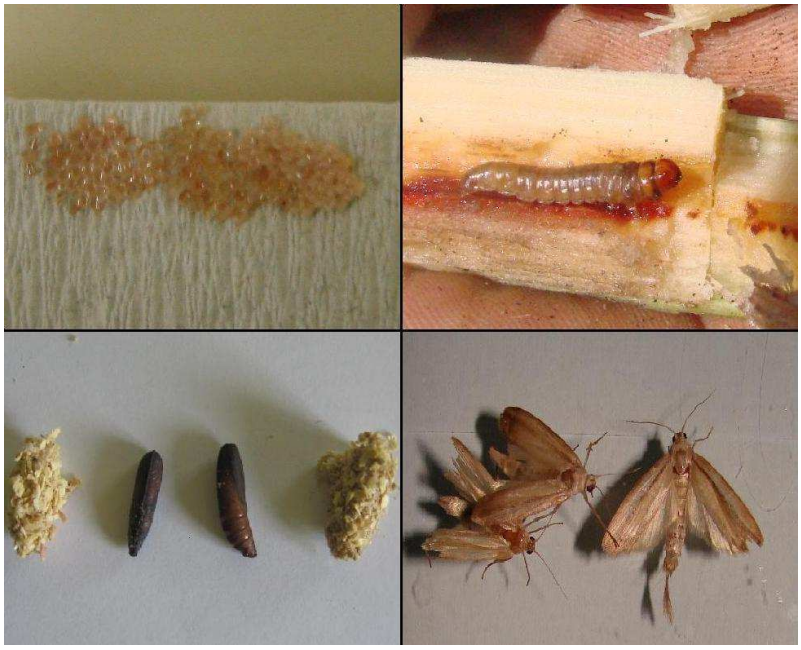


FIGURE 2.3: *Various life stages of E. saccharina include (from top left to bottom right) eggs, larvae, pupae and moths [73].*

as a result of *E. saccharina* boring. Different varieties of sugarcane exhibit different resistance levels to *E. saccharina* infestation. Young larvae experience difficulty in penetrating sugarcane stalks; therefore softer sugarcane varieties are often more infested than the harder varieties [4, 25]. Within each segment of the sugarcane stalk, feeding usually starts around the node, and extends into the internode or throughout the segment. The length of cane damaged by individual larvae is very variable, but between 2 and 8 cm of feeding is required to produce a mature individual [3]. Mature individuals spin cocoons either inside or outside the stalk under the leaf sheath, close to the exit hole, where they spend an inactive pupa stage and from which moths emerge [90]. *E. saccharina* breeds continuously throughout the year. However, seasonal cycles are still observed since particular life stages dominate in different parts of each season. Moth populations peak during early summer and again in autumn, while larval populations peak during the winter months with a smaller peak late during the summer [6, 7, 27]. The autumn moth peak is mainly due to the accumulation of old carry-over cane on the land during the closed mill period. The summer larval peak is generally smaller due to the younger seasonal cane (the older the cane, the more larvae are typically present), whereas the summer moth peak is smaller due to the heavy mortality of the larvae from winter harvesting of carry-over cane. Harvesting of cane is considered the largest mortality factor of *E. saccharina* in sugarcane; natural enemies are not considered a relevant factor [7].

2.2.2 Mating behaviour and movement patterns of adult moths

Moths emerge after sunset, with males emerging slightly before the females [5, 25]. Moths usually mate on the first night of emergence whereafter females begin oviposition for the remainder of their lives [5, 25, 90]. Males usually display in groups of 3–6 moths (*leks*) within the canopy of the sugarcane with very few examples of displaying on their own. A female typically approaches one of these leks and chooses one of the males to mate with. The fairly large size and durability of the spermatophore together with the fact that adult moths have a relatively short lifespan,

FIGURE 2.4: *Damage to sugarcane stalks due to E. saccharina boring [73].*

suggests that females mate only once [5]. According to the latest research, however, the possibility exists that females may mate more than once. A study by Walton [110] confirmed that, under controlled laboratory conditions, males and females are able to mate more than once. The maximum number of matings observed per female was three whereas the maximum number of matings observed per male was six. The majority of females mated only once, whereas the majority of males mated two to three times. Walton suggested that the ability of *E. saccharina* males to mate more than once may reduce the overflooding ratio of sterile males to wild males provided that released males are as competitive than wild males.

E. saccharina seems to be a relatively weak flier [7]. However, research results suggest that some individuals may disperse over considerable distances with the female, being larger and stronger than the male, the more likely to migrate [5, 8]. Atkinson [5] also suggests that migrants may be the more likely individuals that remain unmated at the end of their first or second attempt, in which case approximately one third of females may be involved in dispersal flights at the beginning and end of summer. Another source of migrants may be females searching for oviposition sites. Females usually lay eggs close to their emergence sites, but may fly 200m or more before oviposition [25].

2.2.3 Economic impact

Stalk borers are the most damaging type of insects in African and Indian Ocean Island sugarcane plantations. Studies showed that a reduction in the sucrose content of sugarcane is strongly correlated with damage levels due to *E. saccharina*. *E. saccharina* infestation also impacted negatively on the final sugarcane biomass [7, 35, 44, 59, 65, 112]. Crop and sucrose losses incurred as a result of *E. saccharina* infestation have been estimated at approximately 1% loss in recoverable sucrose for every 1% internodes bored [59], or between 1.0 and 1.5% loss for every 1% stalks red [67]. During the 2001/2002 milling season, the South African sugar industry lost

an estimated R97.4 million to R150 million in revenue due to *E. saccharina* damage [22]. During the 2003/2004 milling season, losses were estimated at R153 million [45].

2.2.4 Strategies to control *E. saccharina* infestation

As a result of the major losses in revenue, effective management of the pest has been the subject of major research activity at SASRI. Since the early 1970s, research has included chemical control [50], crop management [26, 29, 66, 114], varietal resistance [52, 58], biological control [31, 32, 33, 34] and more recently SIT [2].

Insecticide testing has shown that the immersion of seedcane setts in insecticide solutions for 30 minutes reduces the number of larvae, although water accounts for 85% of the mortality. Therefore the effect of insecticide is relatively small [50]. Insecticide deposits on the sugarcane canopy has also proved to be ineffective on moths, but helped reduce larval numbers [50]. As a result of environmental problems associated with the use of pesticides, there has been a global move to reduce reliance on chemical pesticides and to improve the efficiency of pest control programs in an environmentally friendly manner. The development of an effective *integrated pest management* (IPM) system combines biological control, varietal resistance, appropriate farming practices and minimise the use of chemical pesticides [52, 114]. Using information gained from their research, SASRI has been able to develop an IPM for sugarcane farmers in South Africa with suggested control measures. Farming practices that have proved to be effective to some extent include the use of more resistant varieties, early harvesting (since *E. saccharina* infestation increases with crop age), pre-trashing to remove dry leaf material (oviposition sites), the removal of old stalks in the field, the use of clean seedcane and reduced levels of fertilizers containing nitrogen [26, 29, 58, 66, 114].

The current recommended IPM does not yet include the use of natural predators or parasitoids, due to the biological control programme still being in an early research phase. There exist a wide variety of natural enemies of *E. saccharina* which include ants and spiders, with the majority being parasitoids attacking mostly *E. saccharina* larvae [34]. Since 1981 much effort has been devoted to finding appropriate parasitoids from other indigenous host plants, such as *Cyperus papyrus* L, that feed on *E. saccharina*. Despite some limiting factors involving the host plant and climatic incompatibility, some parasitoids have been identified for possible use as biological control agents. However, due to harvesting, no parasitoids have been able to establish themselves in the long term on a sugarcane field [31, 32, 33]. Recent surveys of old sugarcane release sites, however, have since recovered parasitoid where harvesting had been done. The observation by Carl [24] that it took at least 100 generations for a certain parasitoid to change status from incidental parasitoid to a controlling factor may be applicable in the *E. saccharina* case as well [32]. During the search for parasitoids, it was noted that in both sugarcane and papyrus a summer larvae population peak occurs with a second larger peak during winter only in sugarcane. The second peak has been ascribed to harvesting schedules with the accumulation of old carry-over cane on the land during the period when the mills are closed. However, this may also be due to a lack of parasitoids in sugarcane, which are most active during the autumn and winter in papyrus. If indigenous parasitoids can overcome the apparent habitat barrier between sugarcane and papyrus, they may become effective biological control agents in sugarcane [31]. Recent research has shown that sugarcane damaged by *E. saccharina* does not release the same chemical volatiles that damaged papyrus releases. Results from the research indicate that parasitoids need these chemical cues as long-range and short-range signals in order to locate a host habitat and a host within the habitat. This implies that even if parasitoids were to be released in *E. saccharina* infested sugarcane fields, the parasitoids

might be unable to locate their hosts. Further research, such as exposing parasitoids to damaged sugarcane volatiles before release, is necessary in order to improve parasitoid establishment on *E. saccharina* in sugarcane [97].

Another possible source of pest management, namely habitat management, is the concept of using trap crops (or pull plants) to attract insects away from a more valuable crop, and repellent (or push plants) to discourage infestation of the valuable crop. Research results have provided evidence that such habitat manipulation of *E. saccharina* is possible, and that *E. saccharina* seems to exhibit a hierarchical choice of a host plant habitat for ovipositing. Further evidence to promote habitat management as a control option includes the repellent properties of the indigenous African grass *Melinis minutiflora* Beauv. to *E. saccharina* and the fact that *E. saccharina* pupae was parasitised more in sugarcane in the presence of this grass than in pure sugarcane alone [36].

2.3 The Sterile Insect Technique

SIT is a birth control method adopted by entomologists to control pest species either through the release of a large number of laboratory-reared sterile insects into the native population or the sterilization of a proportion of the native population. The sterile organisms mate with fertile organisms to prevent them from reproducing. Sterility in organisms can be obtained by, for example, exposing organisms to gamma rays [62, 87], which is a type of ionising radiation[1].

Three key researchers during the 1930s and 1940s, namely A.S. Serebrovskii (Moscow State University) [62, 92], F.L. Vanderplank (Tsetse Field Research Station in rural Tanganyika) [107] and E.F. Knipling (United States Department of Agriculture) [63] independently conceived the idea to control pest species through the release of sterile populations. It was Knipling's approach, in which he exploited H.J. Muller's discovery that ionizing radiation can induce sterility, however, that has been adopted in several successful area-wide pest control programmes. Examples include the eradication of the New World screwworm *Cochliomyia hominivorax* (Diptera: Calliphoridae) from the USA, Mexico and Central America to Panama, and stopping the invasion of the Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae) from Central America into southern Mexico [62].

SIT is environmentally friendly and is usually applied as a component of AW-IPM. The definition of AW-IPM, due to Klassen [60], is *pest management against an entire pest population within a delimited geographic area, with a minimum size large enough or protected by a buffer zone so that natural dispersal of the population occurs only within this area.* An influx of pests from surrounding areas may prolong the control programme; therefore it is important not to underestimate the flight range of the pest and to include in the programme any nearby microhabitats favourable to the pest from which migrants may enter back into cleared areas. Area-wide control is of considerable importance in the long term if pests are highly mobile and able to migrate to surrounding areas. The lack of control of the onion maggot *Delia antiqua* (Diptera: Anthomyiidae) in the Netherlands is an example of SIT not effectively applied due to the fact that the protected fields did not form a contiguous block. Some growers refused to contribute to the programme, and as a result the programme has not been able to expand beyond 16% of the onion production area [60]. In order to increase the efficiency of SIT,

[1]Ionising radiation induces sterility through dominant lethal mutations which are caused by breakage of chromosomes in germ cells of the irradiated insects. If a sperm carrying these mutations fertilises an egg, the resulting embryo will die. Depending on the dosage of radiation, different levels of sterility can be induced. The higher the dose, the higher the level of sterility [108].

the density of the target pest population may be decreased by other control methods, such as biological control and the use of insecticides, after which SIT imposes birth control on the remaining population to further reduce its numbers. The number of sterile insects released must be sufficiently large in order to overcome the rate of increase of the wild population; therefore it is preferable that the release of sterile insects be initiated when the wild population is at a seasonal low in order to maximise the sterile-to-wild population ratio. Many SIT programmes have failed because too few sterile insects were released. The release ratio must be sustained over several generations for a noticeable effect on the density of the pest [63, 64, 87]. It is also important to maximise the competitiveness or efficiency of a sterilized insect in a control programme so that it is able to compete against the native insects in matings. If a female is polyandrous, the sperm competivity of the sterilized insect should be maintained so as to be able to compete with sperm from untreated males [87].

2.3.1 SIT against Lepidoptera

The development of SIT against Lepidoptera has lagged behind work involving flies due to the fact that large-scale rearing of moths is more difficult than for flies. However, the potential exists and programmes, such as the suppression of the codling moth and pink bollworm, have been successful [62].

Most Lepidoptera require very high doses of radiation compared to other insects (approximately 400 Gy) in order to induce 100% sterility. Physiological damage, such as malformed wings, improper eclosion and the inability to mate, are often the result of high doses of radiation, which in turn affect the competitive ability of released sterile insects compared to their wild counterparts. It has been observed, however, that considerably lower doses of radiation induce partial sterility in male moths and 100% sterility in female moths without debilitating the moths [87]. Low radiation doses, however, appear to have a negative effect on the competitive ability of *E. saccharina* females, with males remaining equally competitive [35, 73]. The F_1 progeny of the partially sterile males (irradiated with sub-sterilizing doses) inherit semi- to complete sterility with the level of sterility of progeny higher than that of the irradiated parent [77, 87]. The radiation doses necessary to induce 100% sterility in *E. saccharina* female moths was found to be 200 Gy whereas the radiation doses necessary to induce inherited sterility in the F_1 progeny of irradiated males was found to be 250 Gy [110]. The sterile F_1 progeny of irradiated males has also been observed to be male-biased with males more sterile than females [77]. This may be due to the induction of recessive lethals on the Z sex chromosome of the male which may result in a higher mortality of the sterile female progeny, resulting in the females able to survive being more fertile than the male progeny. In sugarcane borers, the female and male progeny of irradiated females (with sub-sterilizing doses) have been reported semi-sterile or more fertile than the parent. The higher fertility of offspring from irradiated females (with sub-sterilizing doses) in most lepidopteran species renders it necessary to release partially sterile males instead of females if inherited sterility is the chosen method of suppression. Fully sterile females may be released to aid in the suppression [77]. It is important that no residual fertility occurs in the released sterile females, as this may increase the wild population. Residual fertility in males is less important as this will only reduce the rate at which the population is suppressed [30]. Extended development time and increased mortality in the F_1 progeny of radiated moths have also been observed in previous studies on Lepidopteran species. However, studies on *E. saccharina* development time and survival produced variable data and results were therefore inconclusive [110].

2.3.2 Release strategies

Sterile insects can be used successfully in different types of programmes, including suppression, eradication, containment and prevention. A suppression programme aims to maintain the pest population below an agreed and acceptable economic injury level whereas an eradication programme aims to eliminate the local pest population. Containment programmes are adopted in and around an infested area to prevent the spread of a pest, while measures are applied in and around a pest-free area within prevention programmes in order to avoid the introduction of a pest [108].

The two approaches being followed in the *E. saccharina* SIT project in Kwazulu-Natal, are suppression and prevention. A prevention approach is followed at the pilot site near Eston to form an exclusion zone with the radiated moths to prevent the movement of *E. saccharina* into previously uninfested areas. A suppression approach is followed at the pilot site in Pongola to reduce *E. saccharina* infestations in an already infested area. The sites are surrounded by other land uses; therefore the sugarcane plantations are not contiguous in area, but rather isolated [35].

2.4 Chapter summary

In this chapter, a review of sugarcane in South Africa has been given together with a description of the sugarcane farming context in which SIT will be applied against *E. saccharina*. Biological background information of the lepidopteran specie *E. saccharina* has been presented, which includes the description of the insect's lifecycle, it's population dynamics in sugarcane, mating behaviour and movement patterns. Current strategies to control infestation levels in sugarcane were also reviewed, including early harvesting, pre-trashing, the use of resistant cane varieties and habitat management. Understanding the biology of *E. saccharina* is important in order to formulate a realistic mathematical model of the problem at hand. The chapter concluded with an overview of SIT in general and in specific to lepidopteran species. A summary of the release strategies chosen for the *E. saccharina* SIT project, namely suppression and prevention, was also given.

CHAPTER 3

Survey of mathematical literature

Contents

"Even in literature and art, no man who bothers about originality will ever be original: whereas if you simply try to tell the truth (without caring twopence how often it has been told before) you will, nine times out of ten, become original without ever having noticed it."

— C.S. Lewis

In this chapter a mathematical background is provided with respect to modelling *E. saccharina* population growth, general interaction models of sterile insect releases and a system of partial differential equations which may be used to describe spatial movement. The chapter provides the necessary mathematical foundation to understanding the modelling approach adopted later in this dissertation.

3.1 Population growth models of *E. saccharina*

Very little modelling work has been done specifically related to *E. saccharina* population growth on sugarcane. The first attempts at modelling were those of Van Coller [105] and Hearne *et al.* [49]. The model introduced by Van Coller and by Hearne *et al.* comprises a system of differential equations representing the change in population growth in the various stages of the *E. saccharina* life cycle. The life cycle of *E. saccharina*, as used in the model, is shown in Figure 3.1.

A certain number of stages each represent a specific period in the life cycle of the moth with promotion to subsequent stages occurring at a certain rate, called the *maturation rate*. Each

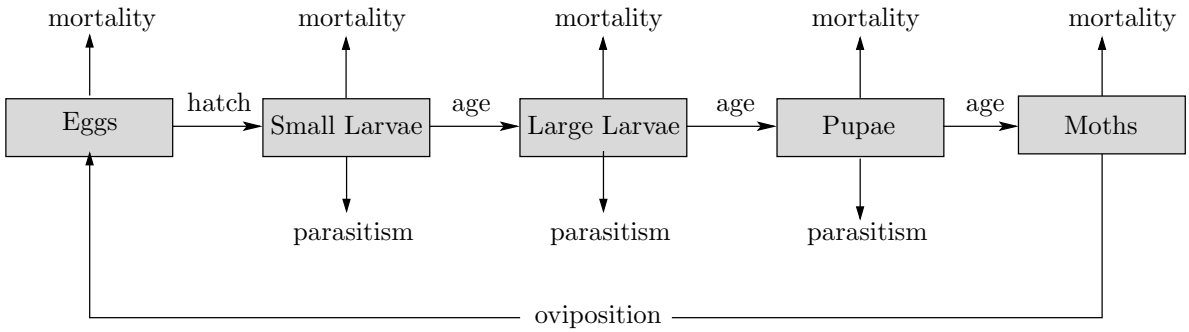


FIGURE 3.1: *Model of E. saccharina life cycle introduced by Van Coller and by Hearne* et al. *[49].*

stage has its own unique temperature-dependent mortality rate. Promotion from the last stage (adult moth) to the first stage (egg) occurs at an *oviposition rate*. The system of model equations is

$$\begin{aligned}
\frac{\mathrm{d}E}{\mathrm{d}t} &= e - h - m_E, \\
\frac{\mathrm{d}S}{\mathrm{d}t} &= h - a_S - m_S - p_S, \\
\frac{\mathrm{d}L}{\mathrm{d}t} &= a_S - a_L - m_L - p_L, \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= a_L - a_P - m_P - p_P, \\
\frac{\mathrm{d}M}{\mathrm{d}t} &= a_P - m_M
\end{aligned}$$

where, together with appropriate initial conditions, E, S, L, P and M denote the population sizes of eggs, small larvae, large larvae, pupae and moths, respectively. Here e denotes the egg laying rate, h denotes the egg hatching rate, and a_S, a_L and a_P denote the stage-specific aging rates. Furthermore, m_E, m_S, m_L, m_P and m_M denote the stage-specific mortality rates, while p_S, p_L and p_P denote the stage-specific parasitism rates. Aging and mortality rates are functions of temperature.

The model provided valuable insight with respect to the biological control of *E. saccharina* through parasitoids. However, no interactions with the host crop were included in the model and temperature effects on the physiological development of *E. saccharina* were also not explicitly included.

A second attempt at modelling the population dynamics of *E. saccharina* was that of Horton [52]. Horton used a simulation model similar to that of Van Coller and Hearne *et al.*, with the exception that difference equations rather than differential equations were used. Also, the main conceptual difference between Horton's model and that of Van Coller and Hearne *et al.* is that physiological age, rather than chronological age, was used. Horton employed a cohort-based structure to keep track of the physiological age of each cohort, where a cohort is defined as all the insects that hatched or matured to the next stage on a specific day. At high temperatures the insects age faster, whereas the insects virtually stop aging when temperatures are too low. Additionally, output from the *CANEGRO model*[1] was used to incorporate interactions with

[1]The CANEGRO sugarcane production simulation model [55] describes environmental, physiological and managerial features of the agricultural sugarcane production system. See the review by Bezuidenhout [18] for further information.

the host crop (see Figure 3.2). Temperature effects on the physiological development of *E. saccharina* in each life-stage were taken into account as well as the effect of the condition of the host sugarcane on the rate of *E. saccharina* infestation. Output parameter values from the *CANEGRO model* that were used are soil-water deficit (crop-water stress), dry leaf matter and the stalk height in order to calculate the condition of the crop, the availability of oviposition sites and the percentage stalk length bored. The oviposition rate was taken to be a function of time, temperature and quality of life (the average crop condition a moth experienced throughout its lifetime). Mortality rates were functions of temperature, crop condition and resistance of the crop variety, while maturation rates were functions of temperature. The model introduced a new criterion (the *crop damage index*[2]) on which to base the *carry-over decision*[3] instead of merely counting the number of pupae in a stalk at the beginning of the carry-over period.

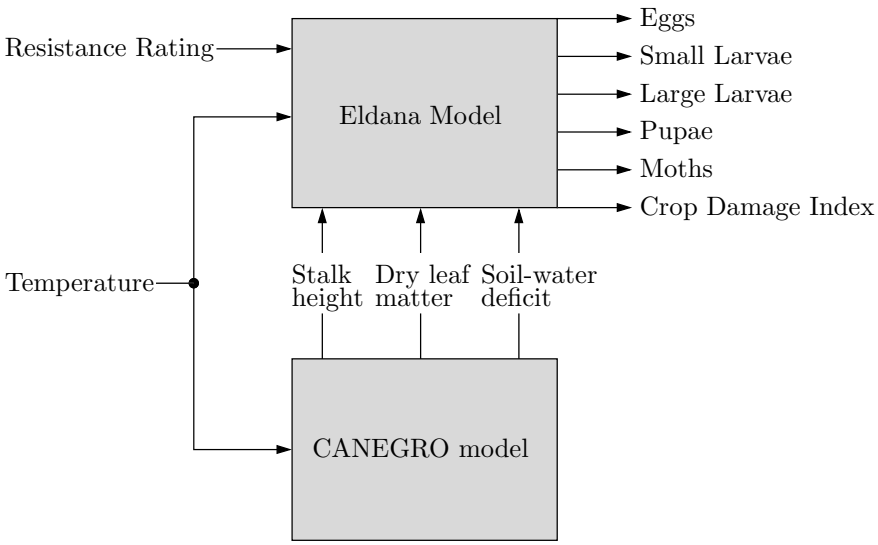


FIGURE 3.2: *Interaction between Horton's [52] E. saccharina model and the CANEGRO model [55].*

The system of equations introduced by Horton is

$$\begin{aligned} E_{i,t+1} &= E_{i,t}(1 - E^m_{i,t} - E^a_{i,t}), \\ S_{i,t+1} &= S_{i,t}(1 - S^m_{i,t} - S^a_{i,t}), \\ L_{i,t+1} &= L_{i,t}(1 - L^m_{i,t} - L^a_{i,t}), \\ P_{i,t+1} &= P_{i,j,t}(1 - P^m_{i,j,t} - P^a_{i,j,t}), \\ M_{i,t+1} &= M_{i,j,k,t}(1 - M^m_{i,j,k,t}) \end{aligned}$$

where, together with appropriate initial values, $E_{i,t}$, $S_{i,t}$ and $L_{i,t}$ represent, on day t, the number of eggs, small larvae and large larvae entering the particular stage on day i, respectively, and $P_{i,j,t}$ represents the number of pupae on day t that matured from large larvae cohort $L_{i,t}$ on day j. Also, $M_{i,j,k,t}$ represents the number of moths on day t that matured from pupae

[2]The crop damage index is defined as an indicator of the damage caused by *E. saccharina*. The crop damage index may also be linked to losses in revenue that are expected if *E. saccharina* populations were left unchecked.

[3]Due to South African mills closing between November and March, a decision has to be made with respect to crops planted late in the season whether to harvest or carry the crop over to March when the mills reopen. This decision is known as the *carry-over decision* and is based on the damage to the crop due to *E. saccharina*. If the damage is expected to reach a certain critical level during the carry-over months, the crop is harvested [52].

cohort $P_{i,j,t}$ on day k. Furthermore, $E^m_{i,t}$, $S^m_{i,t}$, $L^m_{i,t}$, $P^m_{i,j,t}$ and $M^m_{i,j,k,t}$ represent the stage-specific mortality rates and $E^a_{i,t}$, $S^a_{i,t}$, $L^a_{i,t}$ and $P^a_{i,j,t}$ represent the stage-specific maturation rates. Lastly, $E_{t,t} = \sum_k e_{i,j,k,t} M_{i,j,k,t}$ where $e_{i,j,k,t}$ represents the oviposition rate of moth cohort $M_{i,j,k,t}$.

The model underestimated infestation levels, but the timing of the larval peaks coincided with field data. As a result the model is a valuable tool in predicting optimal timing for various control measures. An exploratory spatial model was also introduced, which indicated that neighbouring fields can have a large influence on infestation levels and that certain farming practices may help reduce damage levels to the crop.

3.2 Deterministic vs stochastic time events

For many species, population growth is markedly discontinuous (it occurs in discrete time steps). Species which exhibit discrete population growth are typically those whose members reproduce only once in their lifetimes and die before their descendents' lives begin, as in the case of *E. saccharina* [82]. Despite the fact that births and deaths are stochastic events (chance occurrences), birth and natural death events of these species usually occur at specified times — therefore a deterministic model may be a reasonable approximation. For primitive organisms the discrete time steps can be very short, in which case a continuous (in time) model may also be a reasonable approximation. However, depending on the species, the time step length can vary widely. A common time step length taken is a year. With fruit fly emergence from pupae, the time step length is a day, whereas for cells it can be a number of hours [74]. The model introduced by Horton [52] is both deterministic and discrete, which is reasonable given the fact that and adult *E. saccharina* reproduces only once after which it dies. The deterministic continuous time event models introduced by Van Coller [105] and by Hearne [49] assume that births and deaths occur continuously over time. These are also reasonable approximations given the facts that the life cycle of *E. saccharina* are relatively short, and as a result of individual variations in maturation time, all stages of the *E. saccharina* life cycle are present at all times despite the fact that *E. saccharina* reproduces only once during its life cycle. Either a discrete or continuous model would therefore be good approximations for *E. saccharina* population growth.

3.3 Models of sterile insect releases

In 1955 Knipling [63] examined various basic requirements for pest control by sterile insects and produced a simple modification to the classical geometric growth model

$$N_{t+1} = \lambda N_t, N_0 = \alpha \tag{3.1}$$

in order to estimate the required ratio of fertile:sterile insects. He incorporated a sterility factor $\frac{M_t}{S+M_t}$ in a difference equation of the form

$$F_{t+1} = \lambda F_t \frac{M_t}{S + M_t}, \tag{3.2}$$

where F_t and M_t denote the population sizes of fertile females and males, respectively, at time t, λ is the rate of increase per generation, and S is the number of released sterile males in each generation [63]. The sterility factor represents the probability of a fertile mating.

Numerous modifications to (3.2) have been investigated to incorporate, for example, the problem of residual fertility and reduced competitiveness of sterile insects [12, 13, 17, 61]. The model

introduced by Berryman [17] provided a general mathematical description of the effect of sterile releases in wild populations, and incorporated factors such as residual fertility, competitiveness of males as well as sperm, and the effect on probabilities of sterile matings when matings occur more than once per insect. Berryman modelled the number of adult insects in the generation following the release of sterile insects by means of a difference equation of the form

$$N_{t+1} = N_t F_p E S M_p P_f, \tag{3.3}$$

where N_t denotes the number of wild insects, where F_p denotes the proportion of females in the population, where E denotes the average number of eggs laid per female, where S denotes the proportion of the population that would survive to the next generation, where M_p denotes the proportion of the female population successful in mating and where P_f denotes the probability of a female mating with a fertile male. Berryman also introduced a statistical argument as to finding the value of P_f when an insect can mate more than once.

The earlier models were all based on simple geometric growth. Models which incorporated types of density regulation, as in the classical case of logistic growth, were proposed from the early 1970s onwards by, for example, Miller and Weidhaas [71], Prout [86] and Barclay [10, 11, 12, 15]. Barclay [15] was the first to propose a model in which the dynamics of the released sterile population was also described. Of particular interest to the *E. saccharina* life cycle, sterile releases within insect populations with two life stages have also been considered in the density-dependent models by Miller and Weidhaas [71], Prout [86], and Barclay [11]. The models by Miller and Weidhaas [71] and Prout [86] only considered density-dependence in larval survivorship, while Barclay [11] considered density-dependence in various stages in the life cycle. The density-dependent model of Barclay [11] employs differential equations of the form

$$\begin{aligned}
\frac{\mathrm{d}L}{\mathrm{d}t} &= A(a - b(A+S))(\tfrac{A}{A+S} - L(q + \nu L), \\
\frac{\mathrm{d}A}{\mathrm{d}t} &= L(c - eL) - A(s + \mu(A+S)), \\
\frac{\mathrm{d}S}{\mathrm{d}t} &= r - sS - \mu S(A+S),
\end{aligned}$$

where L, A and S represent the population sizes of larvae, adult insects and released sterile insects, respectively, where a and c denote the density-independent growth rates of the specific stages, and b and e denote density-dependent growth rates. Furthermore, q and s denote density-independent mortality rates of the specific stages, whereas ν and μ denote density-dependent mortality rates. Finally, r denotes the sterile release rate.

One area still largely untapped in the context of sterile releases is the development and use of metapopulation models. A start has been made, however, by introducing immigration and diffusion in some models [14]. Dietz [39] and Prout [86] have investigated two cases of population movement, namely immigration before mating and immigration after mating. When considering immigration before mating, a modification to (3.2) was made by including an immigration term V to arrive at an equation of the form

$$F_{t+1} = \lambda(F_t + V)\frac{M_t + V}{S + V + M_t}$$

where F_t and M_t denote the population sizes of fertile females and males, respectively, at time t, λ is the rate of increase per generation, where V is the number of male and female immigrants and S is the number of released sterile males in each generation. When considering immigration

after mating, (3.2) was modified to

$$F_{t+1} = \lambda F_t \frac{M_t + V}{S + M_t} + \lambda V.$$

For a given value of the immigration rate, the required sterile release rate was found to be much higher if immigration occurs after mating rather than before mating. Large-scale population movement was also studied by, for example, Manoranjan and Van den Driessche [68]. Dispersal of insects, coupled with non-linear diffusion terms, was shown to result in waves of invasion or extinction. The velocity and direction of the waves depend on the rate of release of sterile insects.

3.3.1 Residual fertility

The possibility exists that some of the insects treated are not completely sterilized. Klassen [61] constructed a simple model based on Knipling's model in which a certain proportion of released males remain fertile. He employed a difference equation of the form

$$F_{t+1} = \lambda F_t \frac{M_t + qS}{S + M_t},$$

where F_t and M_t denote the population sizes of fertile females and males, respectively, at time t, λ is the rate of increase per generation, S is the number of released sterile males in each generation and q is the fraction of released males that remain fertile. In terms of the model (3.3), $P_f = \frac{M_t+qS}{S+M_t}$.

Barclay [13] developed a model of the form

$$F_{t+1} = \lambda(F_t + q_f S_f)\frac{M_t + q_m S_m}{S_m + M_t}$$

for the case where both males and females are released and neither sex is completely sterile. Here F_t and M_t again denote the population sizes of fertile females and males, respectively, at time t, λ is the rate of increase per generation, S_f is the number of released sterile females in each generation, S_m is the number of released sterile males in each generation, q_f is the fraction of released females that remain fertile and q_m is the fraction of released males that remain fertile. Barclay [13] found that eradication would be impossible if some of the released sterile males and females are fertile. However, suppression is possible at a critical value $q_m < \frac{F}{\lambda(F+q_f S_f)}$.

3.3.2 Competitiveness of wild vs sterilized males

Sterilization may affect the ability of sterile males to compete with wild males for mates through either sperm competition or adult behaviour. Berryman [17] and Barclay [12] proposed a modification of Knipling's model of the form

$$F_{t+1} = \lambda F_t \frac{M_t}{cS + M_t},$$

where F_t and M_t denote the population sizes of fertile females and males, respectively, at time t, λ is the rate of increase per generation, S is the number of released sterile males in each generation and c is a coefficient of competitive ability, with $c = 0$ representing the case of being completely non-competitive and $c = 1$ the case of being fully competitive. Here, in terms of (3.3), $P_f = \frac{M_t}{cS+M_t}$.

The model showed that the critical release rate increases as the competitive ability of sterilized insects decreases.

3.3.3 Residual fertility and competitiveness

Assuming that residual fertile insects are fully competitive, with a possibility of reduced competitiveness in sterile insects, Barclay [13] suggested a model of the form

$$F_{t+1} = \lambda F_t \frac{M_t + qS}{qS + cS(1-q) + M_t},$$

where F_t and M_t again denote the population sizes of fertile females and males, respectively, at time t, λ is the rate of increase per generation, S is the number of released sterile males in each generation, q is the fraction of released males that remain fertile, and c is the competitiveness coefficient. In terms of (3.3), $P_f = \frac{M_t+qS}{qS+cS(1-q)+M_t}$.

If residual fertile insects exhibit reduced competitiveness as well, the model becomes

$$F_{t+1} = \lambda F_t \frac{M_t + cqS}{cS + M_t},$$

where, in terms of (3.3), $P_f = \frac{M_t+cqS}{cS+M_t}$.

3.3.4 Multiple matings

In the case of insects mating more than once, Berryman [17] noted that the statistical distribution which describes the result of a sterile or fertile mating may be expressed as

$$(P_f + P_s)^r = 1, \tag{3.4}$$

where P_f denotes the probability of an egg being fertilized by fertile sperm, $P_f = 1 - P_s$ and P_s denotes the probability of an egg being fertilized by sterile sperm. Expanding (3.4) for $r = 3$, gives

$$P_f^3 + 3P_f^2 P_s + 3P_f P_s^2 + P_s^3 = 1. \tag{3.5}$$

From this expansion a female may, for example, mate twice with a fertile and once with a sterile male in three different ways.

If fertile and sterile sperm are equally competitive, the probability that a female utilizes sterile sperm would be $\frac{1}{3}$. Therefore, from (3.5), the probability that an egg is fertilized by sterile sperm may be expressed as

$$\frac{1}{3}(3P_f^2 P_s) + \frac{2}{3}(3P_f P_s^2) + P_s^3. \tag{3.6}$$

Substituting $1 - P_s$ for P_f in (3.6) gives

$$\frac{1}{3}(3(1-P_s)^2 P_s) + \frac{2}{3}(3(1-P_s)P_s^2) + P_s^3 = P_s.$$

Therefore, (3.3) remains unchanged if multiple matings occur provided that fertile and sterile sperm are equally competitive.

If, however, sterile sperm is less competitive, the probability that a female utilizes sterile sperm when mating twice with a fertile male and once with a sterile male, would be $\frac{1}{3}c_s$ where c_s denotes the probability ratio of an egg being fertilized by sterile sperm in competition with fertile sperm. The probability that an egg is fertilized by a sterile sperm may now be expressed as

$$\frac{1}{3}(3P_f^2 P_s)c_s + \frac{2}{3}(3P_f P_s^2)c_s + P_s^3. \tag{3.7}$$

Substituting $1 - P_s$ for P_f in (3.7) gives

$$\frac{1}{3}(3(1-P_s)^2P_s)c_s + \frac{2}{3}(3(1-P_s)P_s^2)c_s + P_s^3 = P_s^3 + c_sP_s - c_sP_s^3.$$

This may be expressed in general as $P_s^r + c_sP_s - c_sP_s^r = (1-c_s)P_s^r + c_sP_s$.

Equation (3.3) may therefore be modified to a general expression which considers all possible mating habits and sperm competitiveness as

$$N_{t+1} = N_tF_pES\sum_{r=1}^{R}M_r[1-((1-c_s)P_s^r + c_sP_s)], \tag{3.8}$$

where M_r denotes the proportion of females mating r times [17].

3.4 Reaction-diffusion systems

A change in the concentration of one or more substances distributed across a spatial domain as a result of two processes, namely local reactions in which the particles interact with each other and diffusion[4] across the domain, may be described by mathematical models of the form

$$\frac{\partial w_i(\underline{\xi},t)}{\partial t} = f_i(\underline{\xi},t,w_1,\ldots,w_m) + \nabla\cdot[d_i(\underline{\xi},t)\nabla w_i(\underline{\xi},t)], \qquad i=1,\ldots,m, \tag{3.9}$$

where $w_i(\underline{\xi},t)$ denotes the density of the i–th substance at position $\underline{\xi}$ and at time t, where $\underline{\xi}\in\mathcal{D}$ represents the position of substance particles in a spatial domain $\mathcal{D}$, and where f_i is an expression describing the interaction between the different particles. Futhermore, $d_i(\underline{\xi},t)$ is the diffusion coefficient, which is a measure of how effectively particles of the i–th substance diffuse from a high to a low concentration area in $\mathcal{D}$ at position $\underline{\xi}$ and at time t. Mathematical models of the form (3.9) are referred to as *reaction-diffusion equations*, where the first term on the right hand side describes interaction (or reaction) between substances, and the second term on the right hand side describes movement (diffusion) of the particles [106, 117].

3.4.1 Derivation

As mentioned above, a change in the concentration of one or more substances during time t may be the result of two processes, namely local interaction and movement of the individual particles [93].

Firstly, consider the movement of the particles — it is a natural phenomenon for particles to move from high density regions to low density regions. This movement is called the flux of the population density. Assuming the flux vector $\underline{J}_i(\underline{\xi},t)$ is directly proportional to the spatial gradient of the population density vector, which is the central assumption in Fickian diffusion [116], it follows that

$$\underline{J}_i(\underline{\xi},t) = -d_i(\underline{\xi},t)\nabla w_i(\underline{\xi},t), \tag{3.10}$$

where $d(\underline{\xi},t)$ denotes the diffusion coefficient, which is a measure of how effectively particles of the i–th substance diffuse from high to low density areas at position $\underline{\xi}$ and at time t [93].

[4]Diffusion may be described as the movement of molecules or particles along a concentration gradient without the application of external forces.

Secondly, consider the interaction between particles — the number of particles at any position $\underline{\xi}$ may change because of other reasons than diffusion, such as birth and death processes, or chemical reactions. Assuming that the rate of change in the density of the i–th substance (as a result of the interaction between particles) is given by $f_i(\underline{\xi}, t, w_1, \ldots, w_m)$, then the net growth of the i–th substance in any subset $\mathcal{V} \in \mathcal{D}$ is given by

$$\int_{\mathcal{V}} f_i(\underline{\xi}, t, w_1, \ldots, w_m) \, \mathrm{d}v.$$

By the conservation-of-mass law[5], the rate of change in the density of the i–th substance in any subset $\mathcal{V} \in \mathcal{D}$ is therefore given by

$$\frac{d}{dt} \int_{\mathcal{V}} w_i(\underline{\xi}, t) \, \mathrm{d}v = \int_{\mathcal{V}} f_i(\underline{\xi}, t, w_1, \ldots, w_m) \, \mathrm{d}v - \int_{\partial\mathcal{V}} \underline{J}_i(\underline{\xi}, t) \cdot \mathrm{d}\underline{s}, \tag{3.11}$$

where $d\underline{s}$ is a unit vector orthogonal to $\partial\mathcal{V}$ and pointing outward [106]. The divergence theorem [115] states that

$$\int_{\partial\mathcal{V}} \underline{J}_i(\underline{\xi}, t) \cdot \mathrm{d}\underline{s} = \int_{\mathcal{V}} \nabla \cdot \underline{J}_i(\underline{\xi}, t) \, \mathrm{d}v. \tag{3.12}$$

Substitution of (3.10) and (3.12) into (3.11), and interchanging the order of differentiation and integration yields

$$\int_{\mathcal{V}} \frac{\partial}{\partial t} w_i(\underline{\xi}, t) \, \mathrm{d}v = \int_{\mathcal{V}} \left(f_i(\underline{\xi}, t, w_1, \ldots, w_m) + \nabla \cdot [d_i(\underline{\xi}, t) \nabla w_i(\underline{\xi}, t)] \right) \, \mathrm{d}v$$

when assuming that $w_i(\underline{\xi}, t)$ is once continuously differentiable with respect to t and twice differentiable with respect to $\underline{\xi}$ [106]. Since the subset $\mathcal{V} \in \mathcal{D}$ was chosen arbitrarily, the differential equation

$$\frac{\partial w_i(\underline{\xi}, t)}{\partial t} = f_i(\underline{\xi}, t, w_1, \ldots, w_m) + \nabla \cdot [d_i(\underline{\xi}, t) \nabla w_i(\underline{\xi}, t)]$$

results for any $(\underline{\xi}, t)$. If no reaction occurs, the equation is referred to as a *diffusion equation* [93].

One may also derive the diffusion equation by, instead of applying Fick's law, considering an unbiased random walk[6] — the simplest hypothesis for animal movement [93]. If the movement track consists of a sequence of small steps, it has been shown that by the use of Taylor's theorem, one may also derive a diffusion equation if certain assumptions are made [79, 93]. From this derivation it may be shown that the unit for the diffusion coefficient is $(\text{distance})^2/\text{time}$.

3.4.2 Application in population biology

Many population growth and interaction models employ an underlying assumption that individual organisms encounter one another in proportion to their average abundance across space. This assumption is referred to as the mean-field assumption and is most likely to hold as a good approximation when the physical environment of all organisms is homogenous, forces exist that

[5] The rate of change in the i–th substance in any subset $\mathcal{V} \in \mathcal{D}$ is equal to the 'flow' of the substance across the boundary of $\mathcal{V}$ together with the amount of the i–th substance created per unit volume within $\mathcal{V}$ [106].

[6] A random walk may be defined as the movement of a particle within a spatial domain, which starts at a certain point and takes small successive 'steps' in random directions [93].

cause strong mixing of organisms, high mobility in organisms is evident and interaction with other organisms occurs over long distances. As conditions depart from these, the mean-field assumption becomes less appropriate. Unique neighbourhoods around individuals might exist that deviate from the spatial averages. When interaction occurs only over short distances, differences in local environmental conditions become especially important when the local environment is quite different from the mean environment (averaged across the entire ecological habitat) [38]. In such cases it becomes important to distinguish between different local environments and to adopt a spatially explicit modelling approach, such as the reaction-diffusion system described above.

The similarity between species dispersal in their habitat and the spreading of heat in a plate, as described by equations of the form

$$\frac{\partial n_i}{\partial t} = \nabla \cdot [d(\underline{\xi}, t)\nabla n_i],$$

was first recognised by R.A. Fisher with his application of a diffusion model to the spreading of advantageous genes within a population [42]. The work of Fisher inspired research on the application of reaction-diffusion models to the growth (reaction) and spreading (diffusion) of populations, which may be considered as one the most successful contributions of mathematical theory applied in population biology [106].

3.5 Finite-difference approximations

A numerical method for approximating solutions to systems of partial differential equations such as (3.9), is the finite-difference method. It involves an initial discretization of the domain using finite difference equations to approximate derivatives [21, 96]. Assuming that $\mathcal{D}$ has dimensions $a \times b$, $0 \leq \xi_1 \leq a$ and $0 \leq \xi_2 \leq b$, a rectangular grid topology with grid points of intersections at

$$\begin{aligned} t^k &= kg & (k \geq 0) \\ \xi_1^i &= ih & (0 \leq i \leq m) \\ \xi_2^j &= jh & (0 \leq j \leq n) \end{aligned}$$

may be defined, where $mh = a$ and $nh = b$, which is used to compute approximate values of the solution function w at the grid points.

By Taylor's theorem [118],

$$\begin{aligned} w(\xi_1 + h, \xi_2, t) &= w(\xi_1, \xi_2, t) + hw'(\xi_1, \xi_2, t) + \frac{1}{2}h^2 w''(\xi_1, \xi_2, t) + \mathcal{O}(h^3) \text{ and} \\ w(\xi_1 - h, \xi_2, t) &= w(\xi_1, \xi_2, t) - hw'(\xi_1, \xi_2, t) + \frac{1}{2}h^2 w''(\xi_1, \xi_2, t) + \mathcal{O}(h^3). \end{aligned}$$

Addition of these expansions, and simplifying, yields

$$w''(\xi_1, \xi_2, t) \approx \frac{1}{h^2}\left(w(\xi_1 + h, \xi_2, t) - 2w(\xi_1, \xi_2, t) + w(\xi_1 - h, \xi_2, t)\right),$$

with a leading error of order h^2 [96]. Subtraction of the expansions, on the other hand, yields

$$w'(\xi_1, \xi_2, t) \approx \frac{1}{2h}\left(w(\xi_1 + h, \xi_2, t) - w(\xi_1 - h, \xi_2, t)\right),$$

also with a leading error of order h^2, which is referred to as the *central-difference* approximation. The *forward-difference* approximation is given by

$$w'(\xi_1, \xi_2, t) \approx \frac{1}{h} \left(w(\xi_1 + h, \xi_2, t) - w(\xi_1, \xi_2, t) \right),$$

with a leading error of order h [96].

Assuming that the diffusion coefficient is constant with respect to time and position, approximate values of the derivatives of the solution function w at the grid points are therefore given by

$$\begin{aligned}
\frac{\partial^2 w}{\partial \xi_1^2} &\approx \frac{1}{h^2} \left(w(\xi_1^{i+1}, \xi_2^j, t^k) - 2w(\xi_1^i, \xi_2^j, t^k) + w(\xi_1^{i-1}, \xi_2^j, t^k) \right), \\
\frac{\partial^2 w}{\partial \xi_2^2} &\approx \frac{1}{h^2} \left(w(\xi_1^i, \xi_2^{j+1}, t^k) - 2w(\xi_1^i, \xi_2^j, t^k) + w(\xi_1^i, \xi_2^{j-1}, t^k) \right), \\
\frac{\partial w}{\partial t} &\approx \frac{1}{k} \left(w(\xi_1^i, \xi_2^j, t^{k+1}) - w(\xi_1^i, \xi_2^j, t^k) \right).
\end{aligned}$$

Using the above approximations of the derivatives (*forward-difference method*), the approximate solution to (3.9) has a leading error of order $k + h^2$. The *forward-difference method* has been shown to be conditionally stable, with the method converging to the solution of (3.9) at rate of convergence of $\mathcal{O}(k + h^2)$, provided that $2d^2k \leq h^2$ and the required continuity conditions on the solution are met [21].

3.6 Chapter summary

In this chapter, a review of the mathematical modelling work related to *E. saccharina* population growth on sugarcane has been given. General mathematical models of sterile insect releases have also been discussed, including sterile releases within insect populations with two life stages. Important parameters to take into account when estimating the probabilities of insects mating with fertile and released sterile insects were presented, which include competitiveness, residual fertility, migration and multiple matings. The chapter concluded with a discussion on reaction-diffusion systems — deriving such systems of partial differential equations, their application in population biology and a solution method, called the *finite-difference method*, which may be used to approximate solutions to these systems.

CHAPTER 4

Mean-field model

Contents

"Mathematical modelling is about rules — the rules of reality. Based as it is upon a choice of what to observe and what to ignore, the real-world starting point of any mathematical model must necessarily throw away aspects of this 'real thing' deemed irrelevant for the purposes of the model."

— John Casti

In this chapter a detailed description of the *E. saccharina* population growth model and interaction with sterile released moths is presented. This forms the basis for the spatio-temporal model presented in Chapter 5. After a brief description of the model in §4.1, a list of the model assumptions is given in §4.2. The assumptions made follow from the biological information of *E. saccharina* and SIT contained in Chapter 2, and, in some cases, serve the purpose of simplifying the model. The mathematical formulation of the population growth and interaction model is derived in §4.3 and comprises a discrete and deterministic system of difference equations which is based on logistic growth patterns. In §4.4 the fertilization probabilities are also derived, considering both the probability of mating with a certain type of male (fertile or sterile) and mating with a certain type of female. Previous SIT models only consider the probability of mating with a certain type of male, which does not allow for an analysis of the effect of the sterile released females in an SIT program in cases where both sterile males and females are released. The section closes with a detailed decription of the remaining parameters of the model.

In order to compare the effect of different sterile release strategies, model output parameters are estimated in §4.5 which include the cost of a release strategy, the crop damage index and the increase in revenue expected from such a strategy. In §4.6, simulations are performed in order to verify whether the implementation of the model represents a correct representation of the logic contained in the mathematical description of the model. The model implementation responds as expected to changes in all parameters, thereby verifying the model. The model is also validated in §4.7 by means of data obtained from the Sezela mill and the pilot site near Eston. The optimal release ratio and frequency of releases where suppression is obtained are estimated by means of numerical analysis. The results of this analysis are given in §4.8. A sensitivity analyses is also performed in §4.9 in order to ascertain how robust the optimal strategy is in the face of different parameter values. The chapter closes with a chapter summary in §4.10.

4.1 Description of the model

A model is presented in the following sections to describe the population dynamics of a wild *E. saccharina* population under the influence of a release of fully sterile females and semi-sterile males. The model is discrete and deterministic and comprises a system of difference equations representing the change in population growth over time. It is based on logistic growth patterns. Eleven populations are considered, namely the fertile egg population, the inherited sterile egg population, the newly hatched fertile larvae population outside the stalk, the newly hatched inherited sterile larvae population outside the stalk, the fertile larvae population inside the stalk, the inherited sterile larvae population inside the stalk,the fertile pupae population, the inherited sterile pupae population, the fertile moth population, the inherited sterile moth population and the released sterile moth population (see Figure 4.1). The egg, larvae and pupae stages represent a pre-reproduction stage, while the moth stage represents the reproduction stage in the life cycle of *E. saccharina*. Promotions from stages occur at certain rates, namely the maturation rate and the mortality rate. Each stage is equipped with a distinct temperature-dependent maturation and mortality rate (the rates are functions of temperature).

4.2 Model assumptions

The following model assumptions are made:

1. *Sterility.* The approach followed in the *E. saccharina* SIT project is to radiate moths with sub-sterilising doses which, in turn, result in fully sterile females and partially sterile males [35]. This induces inherited sterility in the F_1 progeny of the partially sterile males. A certain proportion of the F_1 progeny of the partially sterile males are assumed to be 100% sterile, while the rest are assumed to be fertile. For the sake of brevity, partially sterile released moths will be referred to as sterile released moths in this dissertation, or just released moths. It is also assumed that it is possible for a residual proportion of the moths to escape radiation, which will therefore, in fact, be fertile upon release.

2. *Life cycle.* The four stages in the *E. saccharina* life cycle are all divided into separate subpopulations, namely the fertile and sterile populations, in order to keep track of the inherited sterile population. Also, the moth population is divided into three separate subpopulations, namely the wild fertile moth population, the released sterile population and the inherited sterile population.

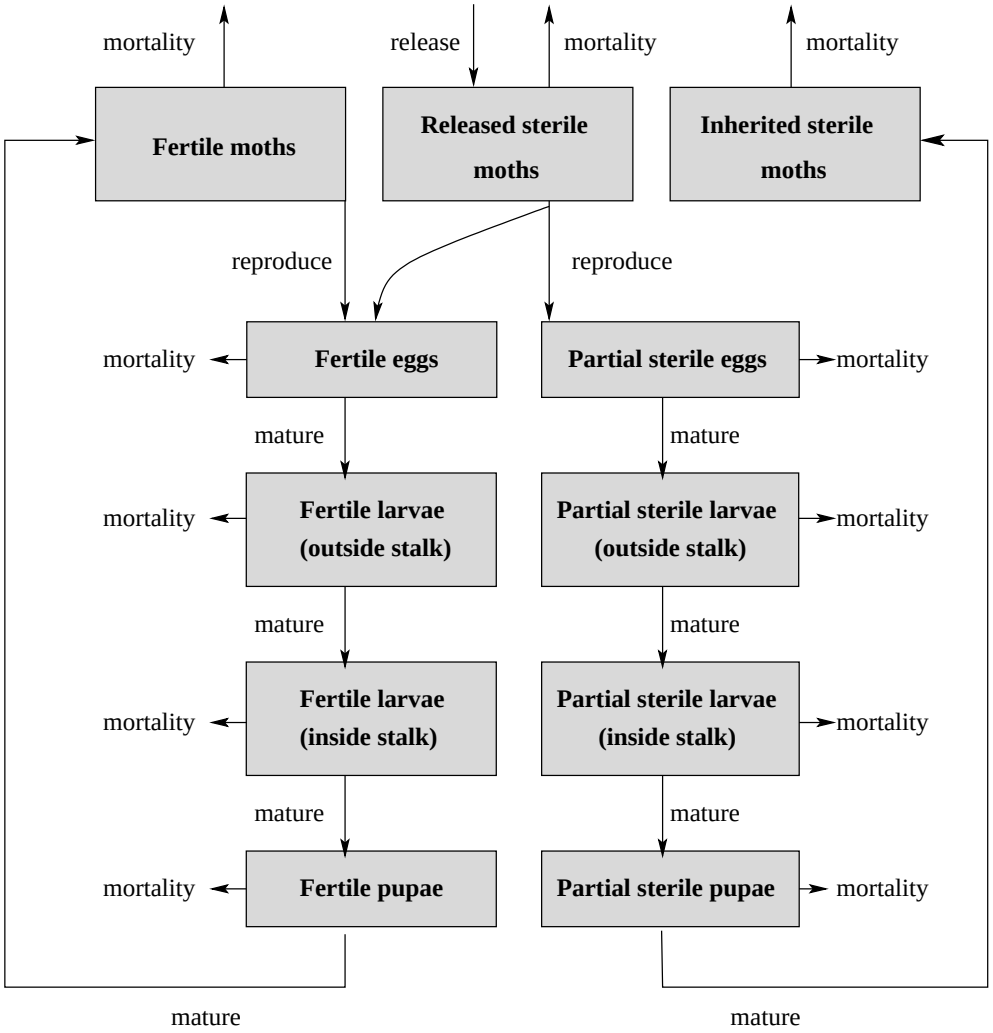


FIGURE 4.1: *Model of E. saccharina life cycle with sterile releases.*

3. *Mating behaviour.* According to the latest research, both females and males are assumed to mate more than once [35], after which the female utilizes some of the sperm to fertilize the egg. Fertile wild moths may either mate with other fertile wild moths, released sterile moths or wild inherited sterile moths.

4. *Gender.* An equal proportion of females and males are assumed in the wild population and released sterile populations. The F_1 generation of a wild-sterile mating is assumed to be male biased as observed in previous studies [30, 35].

5. *Male competitiveness.* Released sterile males are assumed to be less than or equally competitive in attracting females due to the possibility of laboratory, mass-rearing and radiation induced damages and behavioural changes [30]. The F_1 generation of a wild-sterile mating, however, is assumed to be as competitive as the fertile population since they mature in the same environment as the original wild population.

6. *Sperm competitiveness.* The sperm from released sterile males are assumed to be less or equally competitive in fertilizing an egg than the sperm from a wild male. The sperm from a sterile F_1 generation male, however, are assumed to be as competitive as that of a wild male. This is not an unreasonable assumption due to damages caused by radiation in

released sterile males, while the F_1 generation males have experienced the same conditions as the wild fertile males [30].

7. *Reproduction.* Reproduction is assumed to take place when a fertile female utilizes sperm from a wild fertile male or a released sterile male, with no reproduction when sperm from the sterile proportion of the F_1 generation males are utilized. This is a reasonable assumption if it is assumed that released sterile males are semi-sterile and a certain proportion of the F_1 progeny of semi-sterile males are 100% sterile. No reproduction is assumed when a released sterile female mates with any male.

8. *Mortality.* The mortality rate of released sterile moths is assumed to be equal to the mortality rate of wild fertile moths. The mortality rate of the sterile F_1 generation is also assumed to be equal to that of wild fertile generation since they have experienced the same conditions during maturation. The mortality rate of larval populations inside the stalks is assumed to be density-dependent, with a higher mortality at high population levels. This assumption is made due to intraspecific competition (it has been observed that stronger larvae feed on other larvae in the same stalk) [10, 11]. The mortality rates of all populations are assumed to be functions of temperature. This assumption is made according to data from the Entomology Department at SASRI on the stage specific mortality rates of *E. saccharina* and how temperature affects these rates [52].

9. *Growth.* The oviposition rate per female is assumed to be constant over time. However, the oviposition rate per female mating with a released mate is assumed to be less than that of a female mating with a fertile male [110].

10. *Maturation.* Since the time spent in each stage of the *E. saccharina* life cycle is temperature-dependent [52], maturation rates are assumed to be functions of temperature.

11. *Sterile releases.* Releases of sterile moths are assumed to occur at a constant rate over the release period. Releases from an aircraft are assumed with released sterile moths uniformly distributed over the release area. This is a reasonable assumption if the release flight paths are close enough.

12. *Dispersal.* 'Global' dispersal is assumed in the model, where individual organisms encounter one another in proportion to their average abundance across space.

13. *Domain.* A homogenous domain is assumed with regards to cane variety and cane age.

14. *Initial conditions.* In order to solve the model, a certain initial fertile egg population e_1, initial larval population outside the stalks e_3, initial larval population inside the stalks e_5, initial pupal population e_7, initial fertile moth population e_9 and an initial released sterile population e_{11} have to be specified. Initial values of egg, larval, pupal and moth populations are assumed to be in accordance with the relation of the equilibrium population densities of the model. No inherited sterile eggs, larvae, pupae or moths are initially introduced. As sterile releases, new matings and maturation occur in the system, the original wild larvae and moth populations become intermingled with inherited sterile populations.

4.3 Mean-field model

Consider an *E. saccharina* population in its various stages within a closed spatial domain $\mathcal{S}$, which, in the context of this chapter, is assumed to be a sugarcane field with a uniform distribution of *E. saccharina* across the field. Let $E_1(t)$, $E_2(t)$, $E_3(t)$, $E_4(t)$, $E_5(t)$, $E_6(t)$, $E_7(t)$,

$E_8(t)$, $E_9(t)$, $E_{10}(t)$ and $E_{11}(t)$ denote the population densities (e/100s) of the fertile egg population, the inherited sterile egg population, the fertile larval population outside the stalks, the inherited sterile larval population outside the stalks, the fertile larval population inside the stalks, the inherited sterile larval population inside the stalks,the fertile pupal population, the inherited sterile pupal population, the fertile moth population, the inherited sterile moth population and the released sterile moth population at time $t \in [0, 1, \ldots, \infty)$, respectively. Define $\underline{E}(t) = [E_1(t), \ldots, E_{11}(t)]^T$. Furthermore, assume that the change of the population density of the i-th subpopulation per time unit in the field is equal to the amount of the i-th population created per time unit. Then the dynamics of the *E. saccharina* fertile and sterile populations in the various stages may be modelled by means of the temporally discrete reaction equation

$$\underline{E}(t+1) - \underline{E}(t) \quad = \quad \underline{f}(t, \underline{E}), \tag{4.1}$$

where $\underline{f}(t, \underline{E}) = [f_1(t, \underline{E}), \ldots, f_{11}(t, \underline{E})]^T$ contains as its i-th entry the number of the i-th population created during time t. Furthermore, the system of eleven reaction equations is given by

$$\left.\begin{aligned}
f_1(t, \underline{E}) &= 0.5(\gamma(t)\lambda_f + \beta\rho(t)\lambda_s)E_9(t) - (\mu_E(t,\tau) + \alpha_E(t,\tau))E_1(t),\\
f_2(t, \underline{E}) &= 0.5(1-\beta)\rho(t)\lambda_s E_9(t) - (\mu_E(t,\tau) + \alpha_E(t,\tau))E_2(t),\\
f_3(t, \underline{E}) &= \alpha_E(t,\tau)E_1(t) - (\mu_{L_1}(t,\tau) + \alpha_{L_1}(t,\tau))E_3(t),\\
f_4(t, \underline{E}) &= \alpha_E(t,\tau)E_2(t) - (\mu_{L_1}(t,\tau) + \alpha_{L_1}(t,\tau))E_4(t),\\
f_5(t, \underline{E}) &= \alpha_{L_1}(t,\tau)E_3(t) - (\mu_{L_2}(t,\tau)\,(1 + b(t)((E_5+E_6)(t))) + \alpha_{L_2}(t,\tau))E_5(t),\\
f_6(t, \underline{E}) &= \alpha_{L_1}(t,\tau)E_4(t) - (\mu_{L_2}(t,\tau)\,(1 + b(t)((E_5+E_6)(t))) + \alpha_{L_2}(t,\tau))E_6(t),\\
f_7(t, \underline{E}) &= \alpha_{L_2}(t,\tau)E_5(t) - (\mu_P(t,\tau) + \alpha_P(t,\tau))E_7(t),\\
f_8(t, \underline{E}) &= \alpha_{L_2}(t,\tau)E_6(t) - (\mu_P(t,\tau) + \alpha_P(t,\tau))E_8(t),\\
f_9(t, \underline{E}) &= \alpha_P(t,\tau)E_7(t) - \mu_M(t,\tau)E_9(t),\\
f_{10}(t, \underline{E}) &= \alpha_P(t,\tau)E_8(t) - \mu_M(t,\tau)E_{10}(t),\\
f_{11}(t, \underline{E}) &= r(t) - \mu_S(t,\tau)E_{11}(t),
\end{aligned}\right\} \tag{4.2}$$

where λ_f and λ_s denote the egg laying rates of a fertile female mated with a fertile and released male, respectively, $\gamma(t)$ and $\rho(t)$ denote the probabilities of a fertile egg being fertilized by a fertile or semi-sterile sperm at time t, respectively, $\mu_E(t,\tau)$, $\mu_{L_1}(t,\tau)$, $\mu_{L_2}(t,\tau)$, $\mu_P(t,\tau)$, $\mu_M(t,\tau)$ and $\mu_S(t,\tau)$ denote the stage-specific mortality rates at time t and at a temperature of τ degrees. Furthermore, $b(t)$ denotes the density-dependent mortality parameter at time t and $\alpha_E(t,\tau)$, $\alpha_{L_1}(t,\tau)$, $\alpha_{L_2}(t,\tau)$ and $\alpha_P(t,\tau)$ denote the egg, larval and pupal maturation rates at time t and at a temperature of τ degrees, respectively, while $r(t)$ denotes the sterile release rate at time t. Here, β denotes the fraction of eggs from the F_1 progeny of released sterile males which is fertile. Finally, the initial conditions $E_1(0) = e_1$, $E_2(0) = 0$, $E_3(0) = e_3$, $E_4(0) = 0$, $E_5(0) = e_5$, $E_6(0) = 0$, $E_7(0) = e_7$, $E_8(0) = 0$, $E_9(0) = e_9$, $E_{10}(0) = 0$ and $E_{11}(0) = 0$ are prescribed, where e_1, e_3, e_5, e_7 and e_9 are assumed to be positive real numbers [84].

In order to be able to compare solutions of a variety of different scenarios in terms of initial

conditions, equation (4.1) has to be expressed in terms of non-dimensional variables. If we let

$$\mathcal{E}_j(t) = \frac{E_j(t)}{E_j(0)} \text{ and } \mathcal{E}_i(t) = E_i(t)$$

for $i = 2, 4, 6, 8, 10, 11$ and for $j = 1, 3, 5, 7, 9$, where $E_{j(0)}$ denotes the initial fertile population densities at time $t = 0$, then

$$\underline{\mathcal{E}}(t+1) - \underline{\mathcal{E}}(t) = \underline{f}\left(t, \underline{\mathcal{E}}(t)\frac{E_j(0)}{E_i(0)}\right) \tag{4.3}$$

for $i, j = 1, 3, 5, 7, 9$ and

$$\underline{\mathcal{E}}(t+1) - \underline{\mathcal{E}}(t) = \underline{f}\,(t, \underline{\mathcal{E}}(t))$$

for $i, j = 2, 4, 6, 8, 10, 11$.

4.3.1 Initial values

The initial relations between egg, larval, pupal and moth densities are assumed to satisfy the ratios

$$\frac{\lambda_f}{\mu_E + \alpha_E} : \frac{\lambda_f \alpha_E}{(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_1})} : \frac{\mu_M(\mu_P + \alpha_P)}{\alpha_{L_2}\alpha_P} : \frac{\mu_M}{\alpha_P} : 1$$

of the equilibrium population densities in the *E. saccharina* mean-field model. In order to obtain the equilibrium states of the system (4.1), substitution of the time-dependent variables $E_1(t)$, $E_2(t)$, $E_3(t)$, $E_4(t)$, $E_5(t)$, $E_6(t)$, $E_7(t)$, $E_8(t)$, $E_9(t)$, $E_{10}(t)$ and $E_{11}(t)$ by time-independent variables $E_1(t^*)$, $E_2(t^*)$, $E_3(t^*)$, $E_4(t^*)$, $E_5(t^*)$, $E_6(t^*)$, $E_7(t^*)$, $E_8(t^*)$, $E_9(t^*)$, $E_{10}(t^*)$ and $E_{11}(t^*)$ results in the set of equations

$$E_1(t^*) = E_1(t^*) + (\gamma\lambda_f + \beta\rho\lambda_s)E_9(t^*) - \mu_E E_1(t^*) - \alpha_E E_1(t^*), \tag{4.4}$$

$$E_2(t^*) = E_2(t^*) + (1-\beta)\rho\lambda_s E_9(t^*) - \mu_E E_2(t^*) - \alpha_E E_2(t^*), \tag{4.5}$$

$$E_3(t^*) = E_3(t^*) + \alpha_E E_1(t^*) - \mu_{L_1} E_3(t^*) - \alpha_{L_1} E_3(t^*), \tag{4.6}$$

$$E_4(t^*) = E_4(t^*) + \alpha_E E_2(t^*) - \mu_{L_1} E_4(t^*) - \alpha_{L_1} E_4(t^*), \tag{4.7}$$

$$E_5(t^*) = E_5(t^*) + \alpha_{L_1} E_3(t^*) - \mu_{L_2} E_5(t^*)\,(1 + b(E_5(t^*) + E_6(t^*))) - \alpha_{L_2} E_5(t^*), \tag{4.8}$$

$$E_6(t^*) = E_6(t^*) + \alpha_{L_1} E_4(t^*) - \mu_{L_2} E_6(t^*)\,(1 + b(E_5(t^*) + E_6(t^*))) - \alpha_{L_2} E_6(t^*), \tag{4.9}$$

$$E_7(t^*) = E_7(t^*) + \alpha_L E_5(t^*) - \mu_P E_7(t^*) - \alpha_P E_7(t^*), \tag{4.10}$$

$$E_8(t^*) = E_8(t^*) + \alpha_L E_6(t^*) - \mu_P E_8(t^*) - \alpha_P E_8(t^*), \tag{4.11}$$

$$E_9(t^*) = E_9(t^*) + \alpha_P E_7(t^*) - \mu_M E_9(t^*), \tag{4.12}$$

$$E_{10}(t^*) = M_{10}(t^*) + \alpha_P E_8(t^*) - \mu_M E_{10}(t^*), \tag{4.13}$$

$$E_{11}(t^*) = E_{11}(t^*) + r - \mu_S E_{11}(t^*). \tag{4.14}$$

Solving (4.4) to (4.14) simultaneously one obtains the equilibrium states

$$
\begin{aligned}
E_1(t^*) &= \frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_{L_2}\alpha_P}{(\mu_E+\alpha_E)(\mu_P+\alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}\right.\\
&\quad \left.-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{\gamma\lambda_f+\beta\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_2(t^*) &= \frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_{L_2}\alpha_P}{(\mu_E+\alpha_E)(\mu_P+\alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}\right.\\
&\quad \left.-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{(1-\beta)\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_3(t^*) &= \frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_2}\alpha_P}{(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_2})(\mu_P+\alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}\right.\\
&\quad \left.-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{\gamma\lambda_f+\beta\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_4(t^*) &= \frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_2}\alpha_P}{(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_2})(\mu_P+\alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}\right.\\
&\quad \left.-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{(1-\beta)\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_5(t^*) &= \left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{\gamma\lambda_f+\beta\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_6(t^*) &= \left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{(1-\beta)\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_7(t^*) &= \frac{\alpha_{L_2}}{(\mu_P+\alpha_P)}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{\gamma\lambda_f+\beta\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_8(t^*) &= \frac{\alpha_{L_2}}{(\mu_P+\alpha_P)}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{(1-\beta)\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_9(t^*) &= \frac{\alpha_{L_2}\alpha_P}{(\mu_P+\alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{\gamma\lambda_f+\beta\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_{10}(t^*) &= \frac{\alpha_{L_2}\alpha_P}{(\mu_P+\alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f+\beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E+\alpha_E)(\mu_{L_1}+\alpha_{L_1})\mu_{L_2}(\mu_P+\alpha_P)\mu_M}-\frac{\mu_{L_2}+\alpha_{L_2}}{b\mu_{L_2}}\right)\frac{(1-\beta)\rho\lambda_s}{\gamma\lambda_f+\rho\lambda_s},\\
E_{11}(t^*) &= \frac{r}{\mu_S}
\end{aligned}
$$

of each of the eleven populations considered. Grouping each of the subpopulations into eggs, larvae, pupae and moths (excluding the released moths), the equilibrium states for each of the

four different stages in the *E. saccharina* lifecycle are

$$E_1(t^*) + E_2(t^*) = \frac{(\gamma\lambda_f + \beta\rho\lambda_s)\alpha_{L_2}\alpha_P}{(\mu_E + \alpha_E)(\mu_P + \alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f + \beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_1})\mu_{L_2}(\mu_P + \alpha_P)\mu_M} - \frac{\mu_{L_2} + \alpha_{L_2}}{b\mu_{L_2}}\right), \tag{4.15}$$

$$E_3(t^*) + E_4(t^*) = \left(\frac{(\gamma\lambda_f + \beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_1})\mu_{L_2}(\mu_P + \alpha_P)\mu_M} - \frac{\mu_{L_2} + \alpha_{L_2}}{b\mu_{L_2}}\right)\frac{(\gamma\lambda_f + \beta\rho\lambda_s)\alpha_E\alpha_{L_2}\alpha_P}{(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_2})(\mu_P + \alpha_P)\mu_M}, \tag{4.16}$$

$$E_5(t^*) + E_6(t^*) = \left(\frac{(\gamma\lambda_f + \beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_1})\mu_{L_2}(\mu_P + \alpha_P)\mu_M} - \frac{\mu_{L_2} + \alpha_{L_2}}{b\mu_{L_2}}\right), \tag{4.17}$$

$$E_7(t^*) + E_8(t^*) = \frac{\alpha_{L_2}}{(\mu_P + \alpha_P)}\left(\frac{(\gamma\lambda_f + \beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_1})\mu_{L_2}(\mu_P + \alpha_P)\mu_M} - \frac{\mu_{L_2} + \alpha_{L_2}}{b\mu_{L_2}}\right), \tag{4.18}$$

$$E_9(t^*) + E_{10}(t^*) = \frac{\alpha_{L_2}\alpha_P}{(\mu_P + \alpha_P)\mu_M}\left(\frac{(\gamma\lambda_f + \beta\rho\lambda_s)\alpha_E\alpha_{L_1}\alpha_{L_2}\alpha_P}{b(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_1})\mu_{L_2}(\mu_P + \alpha_P)\mu_M} - \frac{\mu_{L_2} + \alpha_{L_2}}{b\mu_{L_2}}\right). \tag{4.19}$$

Note that there are a large number of equilibrium states depending on the set of parameter values, which in turn is temperature and cane variety dependent as well as release ratio dependent. From (4.15) to (4.19) it is possible to find the equilibrium states for both the scenarios with or without sterile releases. In the case of no sterile releases, $\gamma = 1$ and $\rho = 0$. In the case of sterile releases, the inequality $\gamma + \rho < 1$ will hold, which leads to the conclusion that the equilibrium states with sterile releases will always be smaller than without sterile releases. In terms of suppression to any extent, and disregarding the costs involved, it is therefore always more desirable to release steriles.

4.4 Model input parameters

The values of *E. saccharina* population growth parameters used in the model described in §4.3 have all been obtained from previous studies [49, 52, 111], with the exception of the density-dependent mortality parameter $b(t)$. The SIT specific parameters have either been obtained from previous studies [73, 110], or experts' assumptions [35].

4.4.1 Probability of fertilization

A fertile female, a released sterile female or an inherited sterile female may either mate with a fertile male, a released sterile male or an inherited sterile male. This results in nine possible mating combinations.

Definition 4.1 ([46]) *Let P_A and P_B denote the probabilities that two events, A and B, occur. Also, let $P_{A|B}$ denote the conditional probability of A occurring given that B occurs. Then the events A and B are independent if either both events have positive probability and $P_{A|B} = P_A$ and $P_{B|A} = P_B$, or they are independent if at least one of the events has a zero probability.*

Theorem 4.1 ([46]) *Let $P_{A\cap B}$ denote the probability that both the events A and B will occur. The two events A and B are independent if and only if $P_{A\cap B} = P_A P_B$.*

If it is assumed that no type of female has a specific preference for a certain type of male, the conditional probability of mating with a certain type of female given a certain type of male, will be equal to the unconditional probability of mating with a certain type of female given any type of male. Also, if it is assumed that no type of male has a specific preference for a certain type of female, the conditional probability of mating with a certain type of male given a certain type of female, will be equal to the unconditional probability of mating with a certain type of male given any type of female. From Definition 4.1 the events of mating with a certain type of female and mating with a certain type of male are therefore independent if it assumed that no type of male or female has a specific preference for another type of male of female. From Theorem 4.1 the probability of any type of offspring occurring may therefore be calculated by multiplying the probability of mating with a certain type of female with the probability of mating with a certain type of male. Following Berryman [17], the statistical distribution of the nine possible matings may therefore be expressed by

$$(P_{ff}(t) + P_{if}(t) + P_{rf}(t))^n \, (P_{fm}(t) + P_{im}(t) + P_{rm}(t))^n = 1, \tag{4.20}$$

where $P_{ff}(t)$, $P_{if}(t)$, $P_{rf}(t)$, $P_{fm}(t)$, $P_{im}(t)$ and $P_{rm}(t)$ denote the probabilities of mating with a wild fertile female, an inherited sterile female, a released sterile female, a wild fertile male, an inherited sterile male and a released sterile male at time t, respectively, and n denotes the total number of matings possible per insect. Also, the statistical distribution of the three possible matings with a male and female may be expressed separately by

$$(P_{fm}(t) + P_{im}(t) + P_{rm}(t))^n = 1, \tag{4.21}$$
$$(P_{ff}(t) + P_{if}(t) + P_{rf}(t))^n = 1. \tag{4.22}$$

Since the model is only concerned with matings with a fertile female, (4.22) may be rewritten as

$$(P_{ff}(t) + P_{sf}(t))^n = 1, \tag{4.23}$$

where $P_{sf}(t)$ denotes the probability of mating with any type of sterile female at time t. $P_{fm}(t)$ and $P_{sf}(t)$ may be written in terms of $P_{rf}(t)$, $P_{im}(t)$ and $P_{ff}(t)$ as

$$P_{sf}(t) = 1 - P_{ff}(t), \tag{4.24}$$
$$P_{fm}(t) = 1 - P_{im}(t) - P_{rm}(t). \tag{4.25}$$

Furthermore, the expressions

$$P_{rm}(t) = \frac{c_m m\mathcal{E}_{11}(t)(1-q)}{0.5\mathcal{E}_9(t) + c_m m\mathcal{E}_{11}(t) + 0.6\mathcal{E}_{10}(t)}, \tag{4.26}$$

$$P_{im}(t) = \frac{0.6\mathcal{E}_{10}(t)}{0.5\mathcal{E}_9(t) + c_m m\mathcal{E}_{11}(t) + 0.6\mathcal{E}_{10}(t)}, \text{ and} \tag{4.27}$$

$$P_{ff}(t) = \frac{0.5\mathcal{E}_9(t) + c_f q(1-m)\mathcal{E}_{11}(t)}{0.5\mathcal{E}_9(t) + c_f(1-m)\mathcal{E}_{11}(t) + 0.4\mathcal{E}_{10}(t)} \tag{4.28}$$

are assumed, where c_m denotes the competitiveness coefficient of released sterile males, c_f denotes the competitiveness coefficient of released sterile females, q denotes the proportion of residual fertility within the released sterile population and m denotes the male proportion in the released sterile population. An equal proportion of males and females are assumed within the wild fertile population, whereas, the inherited sterile population is assumed to have a 60% male proportion [35]. Furthermore, m may either be equal to 0, 1 or 0.5 depending on whether the released insects are female only, male only, or a combination of female and male, respectively.

The expansion of (4.21) is given by

$$(P_{fm}(t) + P_{im}(t) + P_{rm}(t))^n = \sum_{i=0}^{n}\sum_{j=0}^{n-i} \frac{n!}{i!j!(n-i-j)!} P_{fm}(t)^i P_{im}(t)^j P_{rm}(t))^{n-i-j}, \tag{4.29}$$

where $n-i-j=k$. From (4.29) a female may mate i times with a fertile male, j times with an inherited sterile male and k times with a released sterile male in $\frac{n!}{i!j!k!}$ different sequential orders. If the ability of a released sterile sperm is less than that of a wild sperm, the chance of an egg being fertilized by a fertile sperm is $\frac{i}{n}$, while the probability of an egg being fertilized by a sterile sperm, given that a female has mated with both fertile and sterile males, is $\frac{k}{n}c_s$, where c_s denotes the competitiveness factor of released sterile sperm compared to other sperm. If a female has only mated with sterile moths, the probability of an egg being fertilized by a sterile sperm is 1. The probability of an egg being fertilized by a released sterile sperm may therefore be derived as

$$\begin{aligned}
&P_{rm}(t)^n + \sum_{i=0}^{n}\sum_{j=0}^{n-i} \frac{n!}{i!j!(n-i-j)!} P_{fm}(t)^i P_{im}(t)^j P_{rm}(t)^{n-i-j} \frac{(n-i-j)c_s}{n} - c_s P_{rm}(t)^n \\
&= P_{rm}(t)^n + \sum_{k=0}^{n}\sum_{j=0}^{n-k} \frac{n!}{k!j!(n-k-j)!} P_{rm}(t)^k P_{im}(t)^j P_{fm}(t)^{n-k-j} \frac{kc_s}{n} - c_s P_{rm}(t)^n \\
&= P_{rm}(t)^n + c_s \sum_{k=1}^{n}\sum_{j=0}^{n-k} \frac{(n-1)!}{(k-1)!j!(n-k-j)!} P_{rm}(t)^k P_{im}(t)^j P_{fm}(t)^{n-k-j} - c_s P_{rm}(t)^n \\
&= P_{rm}(t)^n + c_s \sum_{k=0}^{n-1}\sum_{j=0}^{n-k-1} \frac{(n-1)!}{(k)!j!(n-k-j)!} P_{rm}(t)^{k+1} P_{im}(t)^j P_{fm}(t)^{n-k-j-1} - c_s P_{rm}(t)^n \\
&= P_{rm}(t)^n + c_s P_{rm}(t) \sum_{k=0}^{n-1}\sum_{j=0}^{n-k-1} \frac{(n-1)!}{(k)!j!(n-k-j)!} P_{rm}(t)^k P_{im}(t)^j P_{fm}(t)^{n-k-j-1} - c_s P_{rm}(t)^n \\
&= P_{rm}(t)^n + c_s P_{rm}(t) \left(P_{fm}(t) + P_{im}(t) + P_{rm}(t)\right)^{n-1} - c_s P_{rm}(t)^n \\
&= P_{rm}(t)^n + c_s P_{rm}(t) - c_s P_{rm}(t)^n.
\end{aligned} \tag{4.30}$$

Furthermore, the probability of an egg being fertilized by an inherited sterile sperm may be derived as

$$\begin{aligned}
&\sum_{j=0}^{n}\sum_{i=0}^{n-j}\frac{n!}{i!j!(n-i-j)!}P_{fm}(t)^i P_{ism}(t)^j P_{rm}(t)^{n-i-j}\frac{j}{n}\\
&= \sum_{j=1}^{n}\sum_{i=0}^{n-j}\frac{n!}{i!(j-1)!(n-i-j)!}P_{fm}(t)^i P_{im}(t)^j P_{rm}(t)^{n-i-j}\\
&= \sum_{j=0}^{n-1}\sum_{i=0}^{n-j-1}\frac{(n-1)!}{i!(j)!(n-i-j-1)!}P_{fm}(t)^i P_{im}(t)^{j+1} P_{rm}(t)^{n-i-j-1}\\
&= P_{im}(t)\left(P_{fm}(t)+P_{im}(t)+P_{rm}(t)\right)^{n-1}\\
&= P_{im}(t). \qquad (4.31)
\end{aligned}$$

Substituting (4.30) and (4.31) into (4.25) yields the probability of an egg being fertilized by a fertile sperm as

$$1-P_{im}(t)-(P_{rm}(t)^n+c_sP_{rm}(t)-c_sP_{rm}(t)^n),$$

which may be modified to a general expression which considers all possible mating habits (all possible values of n). In general, the probabilities of any egg being fertilized by a fertile and released sterile sperm is given by

$$\sum_{n=1}^{A}F_n[1-P_{im}(t)-(P_{rm}^n(t)+c_sP_{rm}(t)-c_sP_{rm}^n(t))] \qquad (4.32)$$

and

$$\sum_{n=1}^{A}F_n[P_{rm}^n(t)+c_sP_{rm}(t)-c_sP_{rm}^n(t)], \qquad (4.33)$$

respectively, where F_n denotes the proportion of females mating n times and where A denotes the maximum number of matings per female.

The expansion of (4.23) is given by

$$(P_{ff}(t)+P_{sf}(t))^n=\sum_{k=0}^{n}\binom{n}{k}P_{ff}(t)^kP_{sf}(t)^{n-k}. \qquad (4.34)$$

From (4.34) a male may mate with a fertile female and a sterile female in $\binom{n}{k}$ different sequential orders. The probability of any sperm fertilizing a fertile egg may therefore be given by

$$\sum_{k=0}^{n}\binom{n}{k}P_{ff}(t)^kP_{sf}(t)^{n-k}-P_{sf}(t)^n=1-P_{sf}(t)^n. \qquad (4.35)$$

Substituting (4.24) for P_{sf} into (4.35) yields

$$\begin{aligned}
1-(1-P_{ff}(t))^n &= 1-\sum_{k=0}^{n}\binom{n}{k}(-1)^kP_{ff}(t)^k\\
&= -\sum_{k=1}^{n}\binom{n}{k}(-1)^kP_{ff}(t)^k\\
&= \sum_{k=1}^{n}\binom{n}{k}(-1)^{k+1}P_{ff}(t)^k.
\end{aligned}$$

This may be modified to a general expression which considers all possible mating habits (all possible values of n). In general, the probability of any sperm fertilizing a fertile egg may be expressed as

$$\sum_{n=1}^{B} M_n \sum_{k=1}^{n} \binom{n}{k} (-1)^{k+1} P_{ff}(t)^k, \tag{4.36}$$

where M_n denotes the proportion of males mating n times and where B denotes the maximum number of matings per male.

From (4.20) the probability of fertile offspring and inherited sterile offspring may be computed by multiplying the probability of mating with a fertile female (4.36) by the probability of mating with a either a fertile male (4.32) or a released sterile male (4.33), respectively. The probabilities $\gamma(t)$ and $\rho(t)$ are therefore given by [84]

$$\begin{aligned}
\gamma(t) &= \sum_{n=1}^{B} M_n \sum_{k=1}^{n} \binom{n}{k} (-1)^{k+1} P_{ff}(t)^k \sum_{n=1}^{A} F_n [1 - P_{im}(t) - (P_{rm}^n(t) + c_s P_{rm}(t) - c_s P_{rm}^n(t))], \\
\rho(t) &= \sum_{n=1}^{B} M_n \sum_{k=1}^{n} \binom{n}{k} (-1)^{k+1} P_{ff}(t)^k \sum_{n=1}^{A} F_n [P_{rm}^n(t) + c_s P_{rm}(t) - c_s P_{rm}^n(t)].
\end{aligned} \tag{4.37}$$

The values for A, B, F_n and M_n are assumed to be equal to the values obtained in the study by Walton [110] and are summarised in Table 4.1.

Number of matings (n)	M_n	F_n
1	0.1	0.567
2	0.233	0.367
3	0.233	0.066
4	0.167	0
5	0.2	0
6	0.067	0

TABLE 4.1: *The fraction of E. saccharina males (M_n) and females (F_n) exhibiting different mating frequencies (n) with $A = 3$ and $B = 6$.*

4.4.2 Growth rate

Based on model results of VanColler [105] and Horton [52], the number of viable eggs (e/100s) laid per day per female *E. saccharina* moth mated with a fertile male λ_f is assumed to be 4.725. In the study by Walton [110], the number of viable eggs laid per female moth mated with a released male were only 23% of that from a normal fertile mating, therefore λ_s is assumed to be 1.08675.

4.4.3 Stage-specific mortality rates

Each life stage of *E. saccharina* has a unique mortality rate which depends also on the daily average temperature. The Entomology Department at SASRI has, through a number of research experiments, obtained stage-specific mortality rates of *E. saccharina* and how changes in

temperature affect these rates [52]. The stage-specific mortality rates per day of *E. saccharina* at a temperature of $26°C$ are given in Table 4.2. The larval mortality for young larvae was measured higher than the mortality for the more robust larvae which has bored into the sugarcane stalk. Table 4.3 illustrates the change in mortality rate (in relation to mortality rates at a temperature of $26°C$) for each of the specified temperatures.

The sugarcane plant's major defence against *E. saccharina* is to delay stalk penetration and larval activity by physico-chemical factors both on the outside and inside of stalks. Delayed stalk penetration results in longer exposure of larvae to natural and applied mortality factors such as predation and chemical pesticides [58]. Crop varieties have different resistance levels with respect to *E. saccharina* infestation. Higher resistance results in delayed stalk penetration, less larval activity and higher larval mortality inside the stalk. A resistance rating system has been adopted by researchers at SASRI to rate crops according to their resistance against *E. saccharina* infestation. A crop variety with a resistance rating of 1 is considered to be resistant, whereas a crop variety with a resistance of 9 is considered highly susceptible to infestation. Each index rating above 5 is assumed to have 15% more larval activity, which results in a decreased larval mortality of 15%. The larval mortality rate is therefore multiplied by a resistance rating function $v(\omega)$ to incorporate the increase/decrease in mortality for different crop varieties [52].

	eggs (μ_e)	larvae (μ_{l_1})	robust larvae (μ_{l_2})	pupae (μ_p)	moths (μ_m)
Mortality rate (/day)	0.03	0.115	0.009	0.007	0.2

TABLE 4.2: *Stage-specific mortality rates for E. saccharina at a temperature of* $26°C$ *[105].*

	$10°C$	$19°C$	$22°C$	$26°C$	$30°C$
eggs	0.00	0.64	0.78	1.00	1.10
larvae	0.00	0.58	0.78	1.00	1.10
pupae	0.00	0.44	0.54	1.00	1.10
moths	0.00	0.56	0.71	1.00	1.10

TABLE 4.3: *Collocation points for the temperature functions used to adjust mortality rates [105].*

The mortality rate of each specific life stage on a specific day is given by

$$\begin{aligned}
\mu_E(t,\tau) &= \mu_e k_e(\tau), \\
\mu_{L_1}(t,\tau) &= \mu_{l_1} k_l(\tau) v(\omega), \\
\mu_{L_2}(t,\tau) &= \mu_{l_2} k_l(\tau) v(\omega), \\
\mu_P(t,\tau) &= \mu_p k_p(\tau), \\
\mu_M(t,\tau) &= \mu_m k_m(\tau),
\end{aligned}$$

where ω denotes the resistance rating index of the crop variety and the temperature functions $k_e(\tau)$, $k_l(\tau)$, $k_p(\tau)$ and $k_m(\tau)$ are determined by finding the lowest degree polynomial which gives a satisfactory fit to the corresponding stage data in Table 4.3. The lowest degree polynomials giving a satisfactory fit were determined to be of order 6. Changes in the mortality rates $\mu_E(t,\tau)$, $\mu_{L_1}(t,\tau)$, $\mu_{L_2}(t,\tau)$, $\mu_P(t,\tau)$ and $\mu_M(t,\tau)$ as a result of changes in temperature are shown in Figure 4.2.

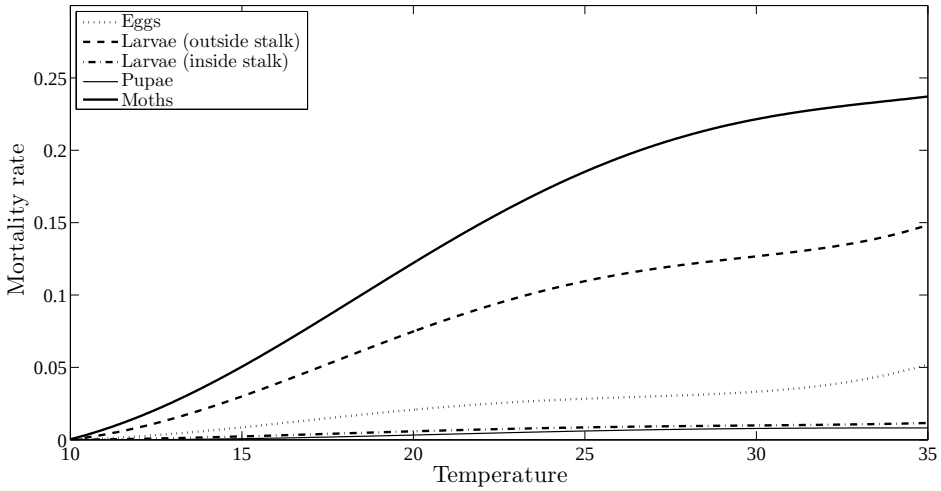


FIGURE 4.2: *The temperature-dependent mortality functions* $\mu_E(t,\tau)$, $\mu_{L_1}(t,\tau)$, $\mu_{L_2}(t,\tau)$, $\mu_P(t,\tau)$ *and* $\mu_M(t,\tau)$.

4.4.4 Density-dependent mortality

Results from surveys have consistently shown that increasing cane age remains the main factor that can be associated with increasing *E. saccharina* infestation [28, 81]. The incidence of *E. saccharina* also appears to be not so much related to the month in which the crop was started, than the age of the crop, and also appears to be independent from the number of ratoons of a crop [81]. During the first few months of sugarcane growth the low nutritional content of immature sugarcane keeps the *E. saccharina* populations low. Infestation levels are typically below 10 e/100s during the first 16 months of growth in two year cycle crop. The last few months of growth and resultant higher nutritional content results in a rapid *E. saccharina* population increase [49]. There is also some evidence to suggest that when *E. saccharina* infestation are low the increase with the age of the cane is not so significant [81]. This may be modelled by assuming a lower carrying capacity and therefore an increased *E. saccharina* larval density-dependent mortality during the first months of sugarcane growth, and also assuming an increased carrying capacity and therefore a decreased *E. saccharina* larval density-dependent mortality during the last few months of sugarcane growth. The value of the density-dependent function, $b(t)$, for any field size is therefore determined, on any specific day, by assuming a decreasing s-shaped function of the form

$$b(t) = \frac{y}{d^z + 1}, \tag{4.38}$$

with $z > 1$ (see Figure 4.3). The maximum value of the function for $0 \leq d \leq 3$ is where $d = 0$ and where $b(0) = y$. In this expression d denotes the expression $\frac{3}{365}a$ for a one-year growth cycle or the expression $\frac{3}{730}a$ for a two-year growth cycle, with a denoting the age of the crop in days at time t. The factor d is used in the expression in order to scale the horizontal axis between 0 and 3 to days. Interaction between *E. saccharina* growth and sugarcane growth, however, is not only dependent upon the age of the sugarcane. Region specific factors, including climate and the type of soil have a major impact on sugarcane growth, which in turn influence the amount of nutrition available to *E. saccharina*. Farming practices, including pretrashing, fertilizing, the use of different cane varieties and field hygiene also has a major impact on *E. saccharina* infestation levels. For the purposes of this study, the above mentioned factors will be incorporated in the model by adjusting the values for y and z in (4.38) according to previous

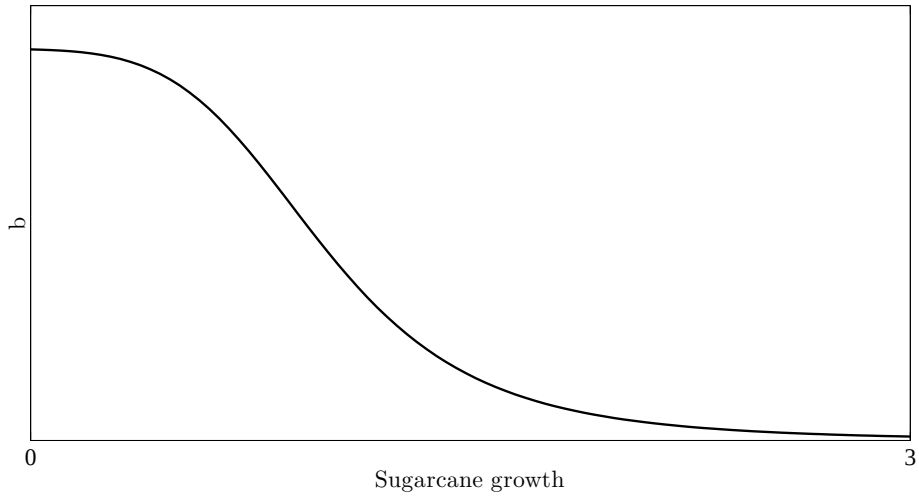


FIGURE 4.3: *The s-shaped function representing the density-dependent mortality parameter, $b(t)$, which decreases as the sugarcane matures.*

infestation data for the specific region.

4.4.5 Stage-specific maturation rates

Maturation from each life stage of *E. saccharina* depends on the temperature to which the insect is exposed. Higher temperatures result in higher rates of maturation until a maximum maturation rate is reached. Entomologists measure insect development (maturation) as the number of *day-degrees* accumulated above a threshold temperature of development. No measurable development occurs below the threshold temperature. The total number of day-degrees required to complete a certain life stage is considered to be a thermal constant. Thermal constants and threshold temperatures of development for each stage (excluding moths) in the *E. saccharina* lifecycle have been calculated at various temperatures through laboratory experiments [111]. In addition, the average time to maturation for each of these temperatures has been calculated and are shown in Table 4.4 together with the corresponding maturation rate approximated by the reciprocal of the average development time. The maturation rate of each specific life stage on a specific day is given by

$$\begin{aligned} \alpha_E(t,\tau) &= g_e(\tau), \\ \alpha_{L_1}(t,\tau) &= g_{l_1}(\tau), \\ \alpha_{L_2}(t,\tau) &= g_{l_2}(\tau), \\ \alpha_P(t,\tau) &= g_p(\tau), \end{aligned}$$

where the temperature functions $g_e(\tau)$, $g_{l_1}(\tau)$, $g_{l_2}(\tau)$ and $g_p(\tau)$ are determined by finding the lowest degree polynomial that gives a satisfactory fit to the corresponding stage data in Table 4.4 (see Figure 4.4).

4.4.6 Competitiveness and fertility of released insects

Even though radiation can cause damage to insects resulting in reduced competitiveness, according to the most recent research, the competitiveness of laboratory-reared *E. saccharina*

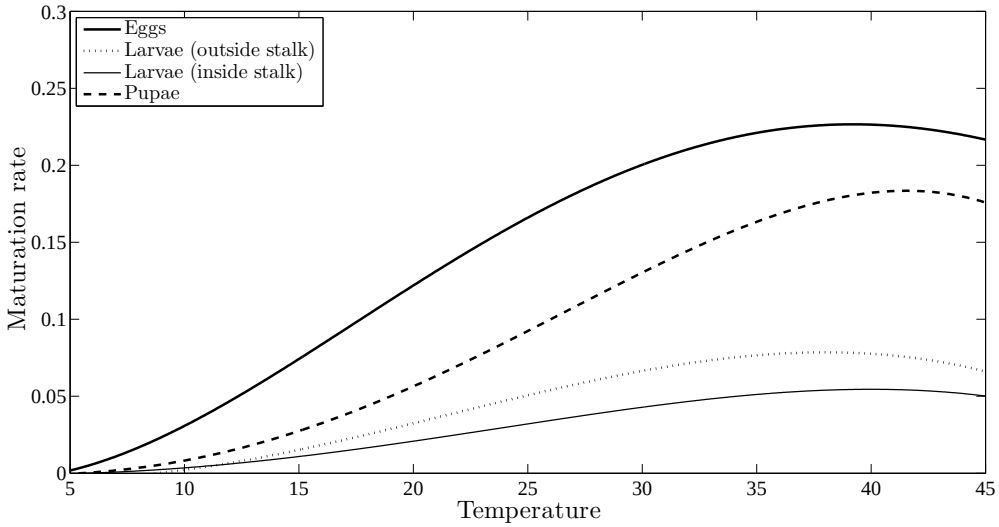


FIGURE 4.4: *The lowest degree polynomials, namely fourth degree polynomials, which give a satisfactory fit to the corresponding stage maturation data.*

	Eggs		**Larvae (outside stalk)**		**Larvae (inside stalk)**		**Pupae**	
$°C$	Days	Rate	Days	Rate	Days	Rate	Days	Rate
13	16.8	0.06						
15	13.2	0.076	85.1	0.01175	97	0.01031	38	0.026
20	8.6	0.116	36.32	0.02753	50.5	0.0198	19.6	0.051
25	6.1	0.164	19.4	0.05155	30.3	0.033	9.8	0.102
30	4.8	0.208	12.7	0.07874	22.9	0.04367	8	0.125
35	4.6	0.217	14.88	0.0672	19.9	0.05025	6.1	0.164

TABLE 4.4: *Average development time (in days) per life stage measured at different temperatures [111]. The maturation rate is approximated by the reciprocal of the average development time spent in each stage.*

males is thought to be more or less the same as for their wild counterparts, and might be even higher. However, the competivity of laboratory-reared *E. saccharina* females seems to be affected to a large extent [73]. Very low radiation doses are required to induce partial sterility to *E. saccharina* males and full sterility to *E. saccharina* females, making it all the more reasonable to assume no measurable reduction in the male competitiveness. Females appear to be more sensitive to radiation, therefore the apparent reduction in their competitiveness [35, 73, 110]. Simulations have therefore been performed assuming the parameters c_m and c_s equal to 1, unless otherwise stated. The value for c_f is assumed equal to 0.1, unless otherwise stated.

As a result of mass radiation, it may be possible for some insects to escape radiation, resulting in a residual number of released steriles remaining fertile [14]. However, with current technology, the fraction of residual steriles, q, is very close to zero and may therefore be ignored [35].

4.4.7 Fertility of the F_1 generation

Experiments have shown, at a radiation dose of $200Gy$, the fraction of fertiles (β) in the F_1 generation from wild females mating with released partially sterile males to be less than 0.15 [110]. As a result of F_1 generation females from wild moths mating with released steriles

being more fertile than the F_1 generation males, fertiles from the F_1 generation have a greater probability to be female, which may result in the fertile moth population becoming female biased. However, since β is so small, the bias in the fertile moth population may be ignored. Steriles from the F_1 generation from wild moths mating with released steriles, on the other hand, have a greater probability of being male, which results in the inherited sterile moth population being male biased. According to research results, the bias in *E. saccharina* is assumed to be approximately 3 : 2 [35].

4.5 Model output parameters

For the purposes of the mean-field model in §4.3, a sterile release strategy is defined as the minimum number, given a certain initial infestation level and frequency of releases, of sterile insects to release in order to suppress a native *E. saccharina* population below 5 e/100s. In order to evaluate the effect of different sterile release strategies on an *E. saccharina* infested area, a crop damage index similar to the index used by Horton in [52] is defined which may serve as an indicator of the damage caused by *E. saccharina*. The crop damage index is also used to estimate the losses in revenue due to *E. saccharina* infestation. In order to compare the benefits from implementing various release strategies, and also to evaluate the economic viability of a release strategy, the estimated cost of the release strategy is compared to the estimated increase in revenue as a result of reduced infestation.

4.5.1 Release strategy

In this chapter, the decision variables, as defined in [80], are the release ratio, η, and frequency of releases in terms of days, θ. Releases are assumed to occur either daily, twice a week, weekly, two weekly, or three weekly and are also assumed to occur either continuously throughout the year, or only during certain months of the year for a set period of time. A release strategy refers to a set of values (η, θ) for both the decision variables. Release strategies started at the beginning of the sugarcane cycle are also compared to strategies started later during the sugarcane cycle. An optimal release strategy is defined as a release strategy which maximises the profit. In order to maximise profit, *E. saccharina* infestation has to be minimised together with the cost of applying SIT. The optimal strategy is obtained by means of simulation.

4.5.2 Cost of release strategy

In order to estimate the cost of a release strategy, three costs are taken into account in this study, namely the cost, κ_r, of raising and sterilising one *E. saccharina* moth, the labour cost, κ_ℓ, involved per day per hectare of releasing sterile moths, and the fuel cost, κ_f, per hectare involved in transporting the sterilised moths on the release site. Transportion cost to a release site is not included in the cost estimation.

The total cost of a release strategy is given by

$$C = \sum_{j=0}^{t} \left(\kappa_r r(j) + (\kappa_\ell + \kappa_f)\phi(j)\right) h \tag{4.39}$$

where $r(j)$ denotes the release rate on day j and calculated by means of the release ratio η, the initial infestation e_9 per 100 stalks, and the number of stalks per hectare. Assuming 130 000

stalks per hectare[1], $r(j) = 1300\eta e_9$. Also, $\phi(j)$ denotes a Bernoulli variable which takes the value 1 if sterile moths are released on day j, and 0 otherwise. Furthermore, h denotes the size (in hectares) of the release site.

There are currently four SIT rearing facilities in South Africa, namely Entomon Technologies (Pty) Ltd, SIT Africa (Pty) Ltd, Xsit (Pty) Ltd and the SASRI Insect Rearing Unit, each producing different types of sterile insect species. The insect species are, in order of the rearing units, the codling moth *Cydia pomonella* (Lepidoptera: Tortricidae), the Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae), the false codling moth *Thaumatotibia leucotreta* (Lepidoptera: Tortricidae) and *E. saccharina*. All of the units, except the SASRI unit, are already commercialised and are mass producing sterile insects, with Xsit (Pty) Ltd achieving the highest production capacity of 18 million moths per week [56]. The higher production capacity a company has, the cheaper the cost per moth becomes. The application of SIT on a farm is currently sold to the farmers as a package deal, which typically comprises twice weekly releases of a minimum of 1 000 moths per hectare (depending on infestation levels) for 7 to 10 months of the year. The total cost to a farmer for applying SIT is currently estimated at between R0.03 and R0.06 per moth released [99, 120]. The SASRI rearing unit is still in the research phase, with limited production capacity. At the time of this study, the cost per sterile *E. saccharina* moth was approximately R1.00, which may reduce significantly once production is increased. In this chapter, κ_r is assumed to range between R0.03 and R0.10.

Aerial releases are considered too expensive below a certain operational scale. The typical costs involved in aerial releases (which include the hiring of an aircraft, fuel and pilot fees) are given as US$465/h [101]. In a large SIT programme in Mexico, releases are performed over a release area of 2 560 ha, at an aircraft speed of 230 km/h and a flight path spacing of 500 m, in a period of 134 min [101]. However, in this dissertation an aircraft speed of 144 km/h is assumed (in accordance with IAEA guidelines [56]). At a cost of US$465/h and a R/US$ exchange rate of 7.37[2], the estimated cost of aerial releases therefore ranges between R4.76 and R23.80 p/ha for a flight path spacing of between 100 and 500 m. Research is still in progress with respect to finding alternative air vehicles which are more cost effective. A recent study proposed a custom-built *unmanned air vehicle* (UAV) which is expected to result in major cost savings in terms of pilot fees and fuel consumption when compared to the aircraft currently used [101]. In this chapter, the aerial release cost $\kappa_\ell + \kappa_f$ is assumed to range between R4.00 and R25.00 per hectare (depending on the type of aircraft used and the flight path spacing).

4.5.3 Crop damage index

In the study by Horton [52], a damage index was defined as the cumulative total of larvae degree-days spent in the sugarcane stalk up to day t. The damage index was used to estimate the total amount of feeding on the sugarcane stalks in a given field since the crop was planted, more specifically, the percentage stalk length bored per field. Varietal screening trials conducted at SASRI have revealed that once *E. saccharina* larvae successfully bore into the sugarcane stalk, more or less the same amount of tissue is consumed. The length of stalk bored per larvae per degree-day is therefore independent of the variety grown, and was found to be, on average, 0.105 mm [52, 57]. The total average length of stalk bored per larvae (assuming a thermal constant of 405 degree-days for robust larvae inside the stalk) is then 42.525 mm. For the purposes of this study, the damage index, $\delta(t)$, on any day t is defined as the cumulative total of larvae feeding

[1] A one hectare field contains, on average, 130 000 stalks in South Africa. An infestation of 1 e/100s is therefore equivalent to 1 300 larvae per ha.

[2] The R/US$ exchange rate on 14 September 2011 [88].

up to day t in a given field since the crop was planted, measured as a percentage of the total of stalk length on day t, and is given by

$$\delta(t) = \frac{\sum_{j=0}^{t} \sigma(j)(\mathcal{E}_5(j) + \mathcal{E}_6(j))}{\ell(t)}, \tag{4.40}$$

where $\sigma(j)$ denotes the amount of larval feeding per larvae on day j and where $\ell(t)$ denotes the average stalk length on day t. In (4.40), σ is an estimation of the length of stalk bored per larvae per degree-day in terms of chronological days. The estimated values for σ for different temperatures are given in Table 4.5. Furthermore, $\ell(t)$ is an estimation (in mm) of the average stalk length on day t given by

$$\ell(t+1) = \ell(t) + 0.16(24)(-1.32 + 0.176(\tau - 10)) \tag{4.41}$$

for a two-year cycle crop, which was obtained from the CANEGRO model [18]. In the CANEGRO model, the stalk development rate is assumed to be 16% of the leaf development rate. Leaf development is assumed to occur in day-degrees, with a threshold temperature of $10°C$. The average stalk length on day t for a one year cycle crop is given by

$$\ell(t+1) = \ell(t) + 0.16(48)(-1.32 + 0.176(\tau - 10)), \tag{4.42}$$

which corresponds to cane growth data from the coastal region in Kwazulu-Natal [44].

$°C$	$\alpha_{L_2}(t,\tau)$	Feeding Rate (mm/day)
15	0.01031	0.4384
20	0.0198	0.842
25	0.033	1.4033
30	0.04367	1.8571
35	0.05025	2.1369

TABLE 4.5: *Average length of stalk bored per larvae per day measured at different temperatures. The feeding rate is approximated by the reciprocal of the average development time spent ($\alpha_{L_2}(t,\tau)$) in each stage multiplied with* 42.525.

4.5.4 Increase in revenue

The South African Sugar Industry has, since the start of the 2000/01 season, adopted the *Recoverable Value* (RV) payment system [23]. The system considers the amount of sucrose, non-sucrose and fibre present in cane delivered at the mill. The RV formula is

$$RV = S - dN - cF, \tag{4.43}$$

where S denotes the percentage of sucrose in cane delivered, d denotes the relative value of sucrose lost from sugar production per unit of non-sucrose (taking into account the value of molasses recovered per unit of non-sucrose) and N denotes the percentage of non-sucrose in cane delivered. Furthermore, c denotes the loss of sucrose from sugar production per unit of fibre and F denotes the percentage of fibre in cane delivered [23]. The parameters c and d vary slightly from mill to mill. The values for c and d assumed in this study are 0.0198 and 0.5506, respectively [52]. The values for N and F are assumed to be equal to the industry averages for

2010, which are 2.61 and 14.6, respectively [70]. The percentage sucrose S of mature sugarcane on day t is given by

$$S = 100\frac{-1.31\delta(t) + 84}{-5.78\delta(t) + 556}, \tag{4.44}$$

where the numerator denotes the sucrose mass in $g/stalk$, while the denominator denotes the stalk mass in $g/stalk$, and where $\delta(t)$ denotes the percentage internodes bored in mature sugarcane on day t. The sucrose mass and stalk mass of the cane was obtained from data of a previous study conducted on sugarcane growth and yield at Gingindlovu, Kwazulu-Natal [44]. The relationship between the percentage sucrose, S, and the percentage internodes bored, $\delta(t)$, is illustrated in Figure 4.5.

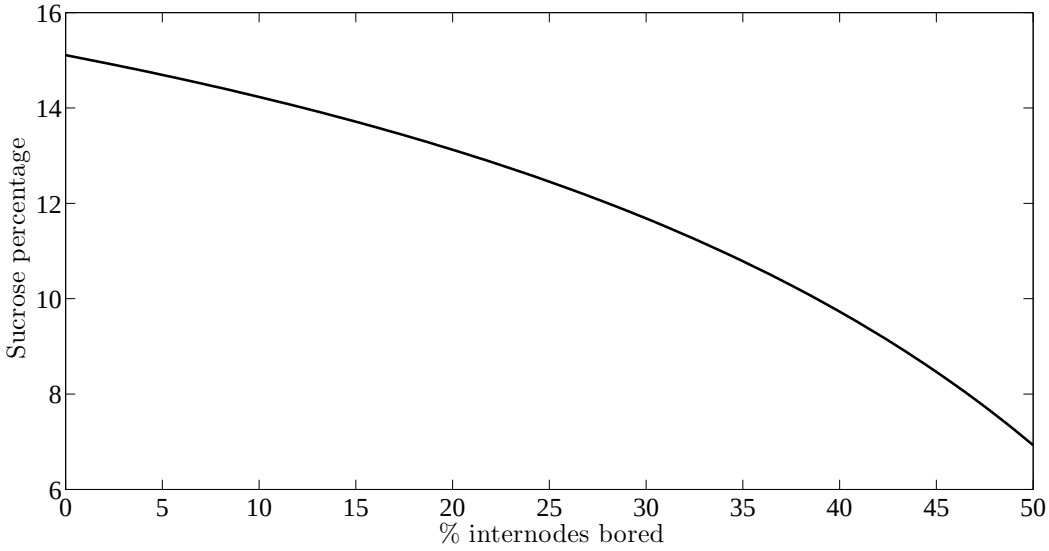


FIGURE 4.5: *The relationship between sucrose percentage in cane delivered and the percentage of internodes bored [44].*

In order to calculate the payment due to a farmer, the RV percentage obtained from (4.43) is multiplied by the number of tons of sugarcane delivered and the RV price [19]. For the purposes of this study, the RV price per ton of the 2011/2012 milling season, which was recorded at R2817.05, is assumed. The revenue W is therefore given by

$$W = 2817.05T\frac{RV}{100}, \tag{4.45}$$

where T denotes the average number of tons of sugarcane delivered, namely $0.13h(-5.78\delta(t) + 556)$. The relationship between the revenue per hectare, W, and the percentage internodes bored, $\delta(t)$, is illustrated in Figure 4.6.

Using (4.43), (4.44) and (4.45), the revenue in 2011 for a 1 ha field where no *E. saccharina* infestation occurs is estimated at R27 247.47 for an average of 72.28 tons delivered per hectare, which gives an average of R376.97 per ton delivered. For every 1% internode damage, there is an expected decrease of 1.6% in the estimated revenue. In order to estimate the increase in revenue for a certain SIT release strategy, the estimated revenue with no SIT measures applied will be compared to the estimated revenue if a certain SIT strategy is applied. The increase in revenue as a result of SIT is given by

$$I = W_{SIT} - W, \tag{4.46}$$

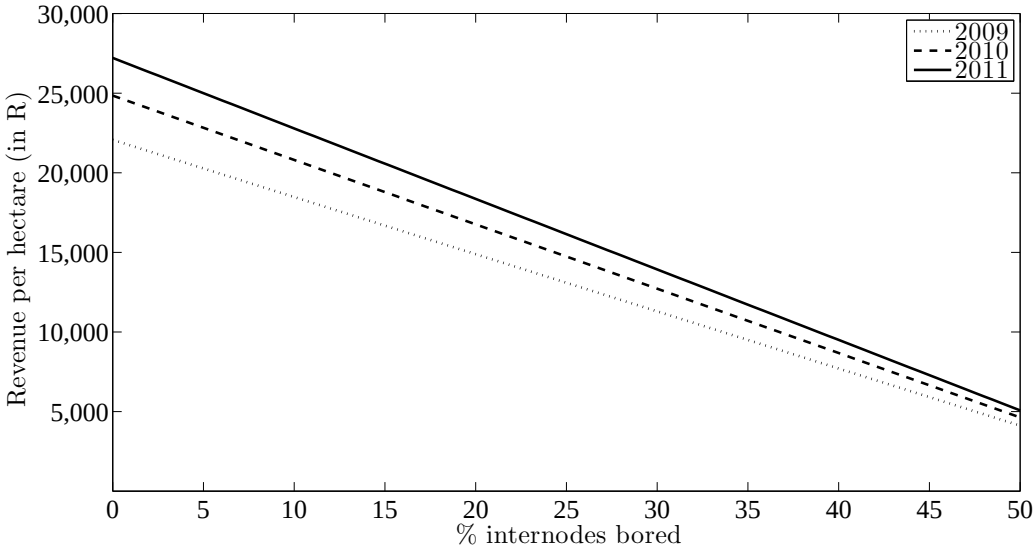


FIGURE 4.6: *The relationship between the revenue per hectare for cane delivered and the percentage of internodes bored assuming the 2009, 2010 and 2011 RV prices of R2284.20, R2572.14 and R2817.05, respectively.*

where W_{SIT} denotes the revenue if a certain SIT strategy is applied. The profit made as a result of SIT is given by

$$P = I - C. \tag{4.47}$$

4.6 Model verification

Before sensitivity analyses may be performed by means of an implementation of the model in §4.3, it is necessary to verify whether the implementation of the model represents a correct representation of the logic contained in the mathematical description of the model. This may be achieved by verifying whether the model implementation's response to the various parameters is as expected. The model was implemented in Mathworks' MATLAB (R2009a) and all simulations reported here were performed for a field size of 1 ha.

The parameters τ and ω have an effect on the maturation time and mortality of *E. saccharina*. For high values of τ, the development time in each life stage will be shorter than for low values of τ, resulting in infestation levels increasing faster. The mortality rates also increase as τ increases, resulting in lower levels of infestation. As a result of less larval activity in the more resistant sugarcane varieties, the *E. saccharina* infestation level is expected to be lower for $\omega < 6$ when compared to infestation levels if $\omega \geq 6$. The parameters c_m, c_f, c_s, f, q and r have an effect on the *E. saccharina* infestation level after sterile releases. An inverse relationship between c_m and c_f and the infestation level, and between c_s and the infestation level is expected due to the reduced effectiveness of the released sterile insects. A direct relationship between f and the infestation level, and between q and the infestation level is expected whereas an inverse relationship between the release rate r and the infestation level is expected.

4.6.1 Model response to τ

In order to test whether the model implementation responds correctly to changes in temperature, simulations were performed without any sterile releases, and with temperatures held constant at $20°C$ and $30°C$ over a time period of 2 years. Initial larval infestation levels were chosen as 0.1 e/100s stalks, with appropriate initial values for egg, larvae, pupae and moth populations. In order to test whether the model responds correctly to different maturation rates, mortality rates were kept constant for both temperatures. In order to test whether the model responds correctly to different mortality rates, maturation rates were kept constant for both temperatures. As may be seen in Figure 4.7, when mortality rates are kept constant, infestation levels are much lower at $20°C$ compared to infestation levels at $30°C$. This is expected, since maturation rates at $20°C$ are much lower than maturation rates at $30°C$, which results in infestation levels increasing slower. When maturation rates are kept constant, infestation levels are much higher at $20°C$ compared to infestation levels at $30°C$. This is expected, since mortality rates at $20°C$ are much lower than mortality rates at $30°C$, which results in infestation levels being higher. The model implementation, therefore, responds as expected when tested for its response to various temperature conditions.

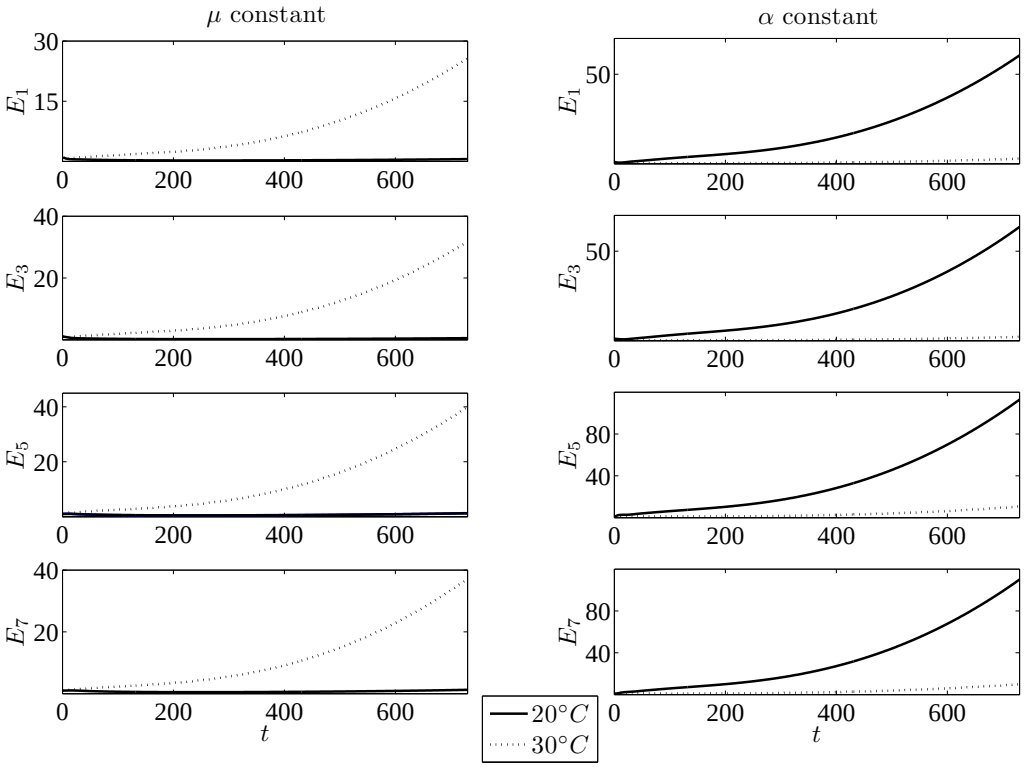


FIGURE 4.7: *Simulation results of E. saccharina populations illustrating the model implementation response to temperature variation.*

4.6.2 Model response to m

It is expected that, if the released female competitiveness is equal to 0, the model with both male and female releases should suppress an *E. saccharina* population with double the amount of moths needed than if only males were released. In order to test whether the model implementation responds correctly to changes in the proportion of released sterile males, simulations

were performed over a time period of 24 months with initial population levels chosen as 0.1 e/100s and appropriate initial values for larvae, pupae and moth populations. The fertile proportion of the F_1 generation of released sterile males was set equal to 0.1, the residual fertility in released moths was set equal to 0, the male and female competitiveness was set equal to 1 and 0, respectively, and sterile releases included either males and females or just males. The release ratio necessary to suppress an *E. saccharina* infestation below 5 e/100s with daily sterile releases of males and females is 0.102 : 1, whereas the release ratio necessary to suppress an *E. saccharina* infestation below 5 e/100s with daily sterile releases of only males is 0.051 : 1. The model implementation, therefore, responds as expected when tested for its response to either male only or male and female releases with female competitiveness equal to 0.

4.6.3 Model response to η

In order to test whether the model implementation responds correctly to changes in the release rate of released sterile moths, simulations were performed with daily sterile releases at a ratio of 0.2 : 1 and 0.5 : 1 of the moth population on day 1, respectively, over a time period of 24 months. Initial population levels were chosen as 0.1 e/100s, with appropriate initial values for larvae, pupae and moth populations. The fertile proportion of the F_1 generation of released sterile males was set equal to 0.1, the residual fertility in released moths was set equal to 0, the male and female competivity was set equal to 1 and 0.1, respectively, and sterile releases included males and females. Infestation was observed to decrease faster for larger values of the release rate (see Figure 4.8). The model implementation, therefore, responds as expected when tested for its response to various levels of sterile releases.

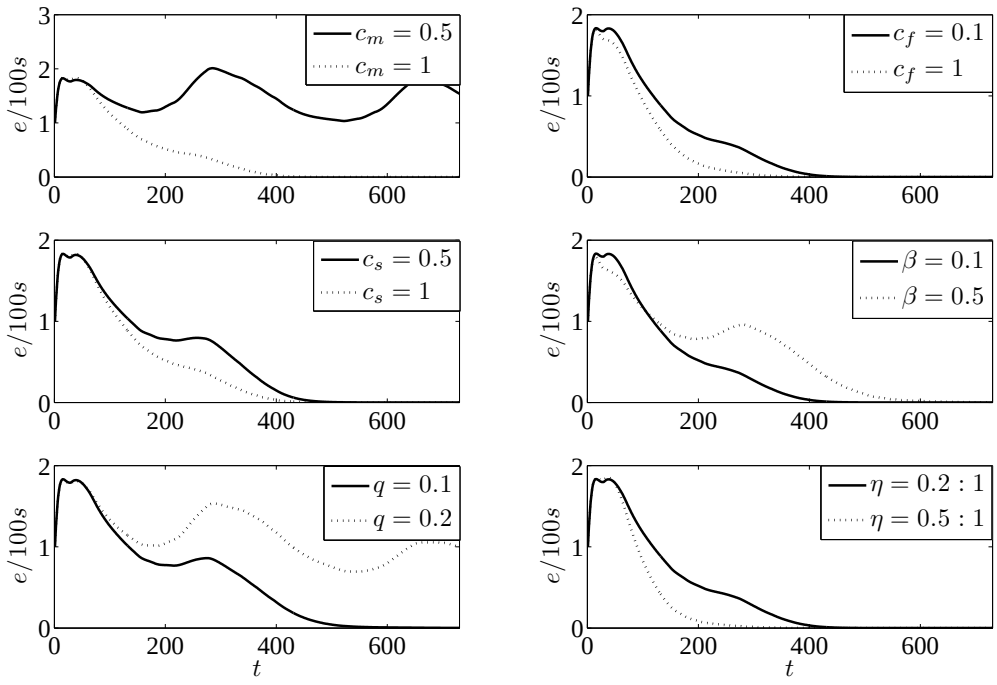


FIGURE 4.8: *Simulation results of larval populations illustrating the model implementation response to changes in the parameters c_m, c_f, c_s, β, q and η.*

4.6.4 Model response to ω

In order to test whether the model implementation responds correctly to changes in the crop variety, simulations were performed without sterile releases over a time period of 24 months with the resistance rating set equal to 5 and 8, respectively. Initial infestation levels were chosen[3] as 0.1 e/100s, with appropriate initial values for egg, larvae, pupae and moth populations. Larval populations increase to much higher levels of infestation for higher values of ω, which corresponds to more susceptible crop varieties (see Figure 4.9). The model implementation, therefore, responds as expected when tested for its response to changes in the crop variety.

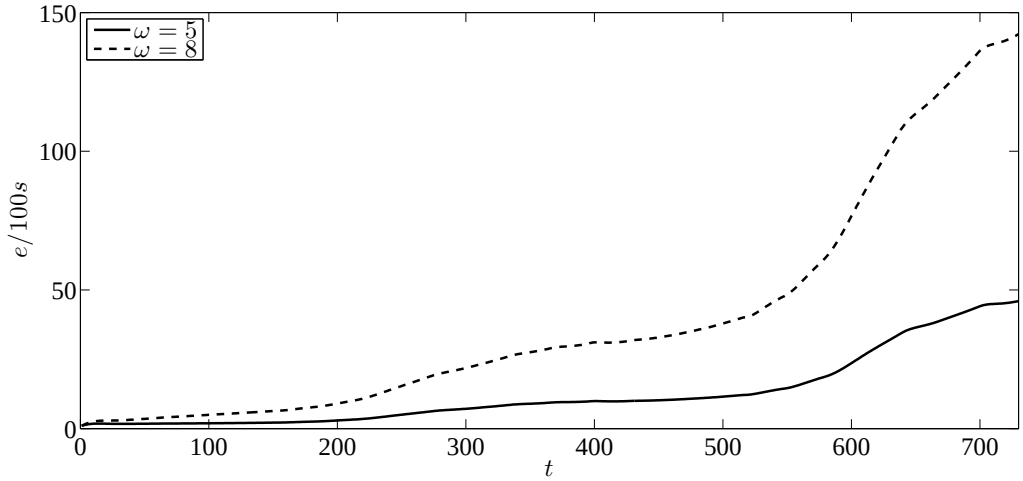


FIGURE 4.9: *Simulation results of larval populations illustrating the model implementation response to* ω.

4.6.5 Model response to c_m

In order to test whether the model implementation responds correctly to changes in the competitiveness of released sterile males, simulations were performed with daily sterile releases at a ratio of 0.2 : 1 of the moth population on day 1 over a time period of 24 months. Initial population levels were chosen as 0.1 e/100s, with appropriate initial values for egg, larvae, pupae and moth populations. The fertile proportion of the F_1 generation of released sterile males was set to 0.1, the residual fertility in released moths was set to 0 and sterile releases included males and females. The competitiveness of released sterile males was set to 0.5 and 1, respectively, whereas female competitiveness was set to 0.1. Infestation levels were observed to decrease to low levels faster under higher levels of competitiveness of released sterile males (see Figure 4.8). The model implementation, therefore, responds as expected when tested for its response to various male competitiveness coefficients.

4.6.6 Model response to c_f

In order to test whether the model implementation responds correctly to changes in the competitiveness of released sterile males, simulations were performed with daily sterile releases at a ratio of 0.2 : 1 of the moth population on day 1 over a time period of 24 months. Initial population levels were chosen as 0.1 e/100s, with appropriate initial values for egg, larvae, pupae and

[3]Infestation levels are given as the number of *E. saccharina* per 100 stalks, which includes the number of large larvae found per 100 stalks in an infested sugarcane field.

moth populations. The fertile proportion of the F_1 generation of released sterile males was set to 0.1, the residual fertility in released moths was set to 0 and sterile releases included males and females. The competitiveness of released sterile females was set to 0.5 and 1, respectively, whereas male competitiveness was set to 1. Infestation levels were observed to decrease to low levels faster under higher levels of competitiveness of released sterile females (see Figure 4.8). The model implementation, therefore, responds as expected when tested for its response to various female competitiveness coefficients.

4.6.7 Model response to c_s

In order to test whether the model implementation responds correctly to changes in the competitiveness of sperm of released sterile moths, simulations were performed with daily sterile releases at a ratio of $0.2 : 1$ of the moth population on day 1 over a time period of 24 months. Initial population levels were chosen as 0.1 e/100s, with appropriate initial values for larvae, pupae and moth populations. The fertile proportion of the F_1 generation of released sterile males was set to 0.1, the residual fertility in released moths was set to 0, the male competitiveness was set to 1, female competitiveness was set to 0.1, and sterile releases included males and females. Infestation levels were observed to decrease to low levels for all sperm competitiveness coefficients, with a faster decrease in infestation for a sperm competitiveness coefficient of 1 (see Figure 4.8). The model implementation, therefore, responds as expected when tested for its response to various sperm competitiveness coefficients.

4.6.8 Model response to q

In order to test whether the model implementation responds correctly to changes in the residual fertility of released sterile moths, simulations were performed with daily sterile releases at a ratio of $0.2 : 1$ of the moth population on day 1 over a time period of 24 months. Initial population levels were chosen as 0.1 e/100s, with appropriate initial values for larvae, pupae and moth populations. The fertile proportion of the F_1 generation of released sterile males was set to 0.1, the residual fertility in released moths was set to 0.1 and 0.2, respectively. Futhermore, the male and female competivity was set equal to 1 and 0.1, respectively, and sterile releases included males and females. Infestation levels were observed to be higher for larger values of residual fertility (see Figure 4.8). The model implementation, therefore, responds as expected when tested for its response to various residual fertility values.

4.6.9 Model response to β

In order to test whether the model implementation responds correctly to changes in the fertility of the F_1 generation of released sterile males, simulations were performed with daily sterile releases at a ratio of $0.2 : 1$ of the moth population on day 1 over a time period of 24 months. Initial population levels were chosen as 0.1 e/100s, with appropriate initial values for larvae, pupae and moth populations. The fertile proportion of the F_1 generation of released sterile males was set to 0.1 and 0.5, respectively. Furthermore, the residual fertility in released moths was set to 0, the male and female competivity was set equal to 1 and 0.1, respectively, and sterile releases included males and females. Infestation levels were observed to be higher for larger values of fertility in the F_1 generation (see Figure 4.8). The model implementation, therefore, responds as expected when tested for its response to various levels of fertility in the F_1 generation of released sterile males.

4.7 Model validation

Model validation may be understood as the process of showing that a model possess a satisfactory range of accuracy, within its domain of applicability, consistent with the intended application of the model [52]. The intended application of the model described in §4.3, is to investigate the population decline in a native *E. saccharina* population as a result of sterile insect releases into the native population. The *E. saccharina* life cycle under various temperature and crop conditions was incorporated into the model, albeit in very simplified terms. However, any mathematical model must necessarily make simplifying assumptions in order to describe a part of a real-world process. The model in §4.3 describes interaction between *E. saccharina* growth and sugarcane growth with the use of a decreasing density-dependent mortality function (4.38) which only depends on the age of the sugarcane, disregarding any other factors (such as rainfall) which may have influenced the quality of the sugarcane and, in turn, the amount of nutrition available to *E. saccharina*. Furthermore, the model disregards any farming practices which may have resulted in different responses in the attack rate on sugarcane by *E. saccharina*. As mentioned in §4.4.4, for the purposes of this study, the above mentioned factors are incorporated into the model by adjusting the values of y and z in (4.38) according to previous infestation data for the specific region.

In order to determine whether the model described in §4.3 provides a satisfactory representation of *E. saccharina* infestation in sugarcane in South Africa, the model was tested against data sets obtained from the Sezela mill [70], where infestation is considered fairly low. All simulations reported here were performed for a field size of 1 ha over a time period of 24 months, with initial population levels chosen as 0.1 e/100s and appropriate initial values for larvae, pupae and moth populations. The fertile proportion of the F_1 generation of released sterile males was set equal to 0.1, the residual fertility in released moths was taken as 0, the male and female competitiveness were set equal to 1 and 0.1, respectively, sperm competitiveness was taken as 1, and sterile releases included males and females.

Data obtained from the Sezela mill for 2010 indicates an average of 3.78 e/100s at an average cane age of 13.6 months. The cane in the Sezela region matures between 18 and 24 months, but farmers cut cane at younger ages to prevent high levels of *E. saccharina* infestation. The average percentage stalks red was measured at 2.08% [70], which is equivalent to the average percentage of internodes damaged [44]. The model without sterile releases, when assuming a density-dependent mortality function

$$b(t) = \frac{10}{(d^{2.5} + 1)}, \tag{4.48}$$

where d denotes the expression $\frac{3}{365}a$ for a one-year growth cycle or the expression $\frac{3}{730}a(t)$ for a two-year growth cycle, with $a(t)$ denoting the age of the crop in days at time t, gives an *E. saccharina* infestation of 4 e/100s at 13.6 months corresponding to the Sezela data, which then increases to 18.39 e/100s at the end of a 24 month cycle (see Figure 4.10). The percentage internodes damaged given by the model, however, underestimates the internode damage due to *E. saccharina*. At 13.6 months the percentage internodes damaged are given as 0.85% and at 24 months as 2.16% (see Figure 4.10). One of the reasons why the model may underestimate the percentage damage, is due to the fact that the model assumes ideal growth conditions for cane. During 2010 the area around the Sezela mill experienced low rainfall. Stalks under stressed conditions (low rainfall) have lower height than in ideal conditions, and is much more vulnerable to *E. saccharina* infestation. A stalk height of 0.7 m at maturation is not uncommon in stressed cane [35]. Another reason why the model may underestimate the percentage damage is that

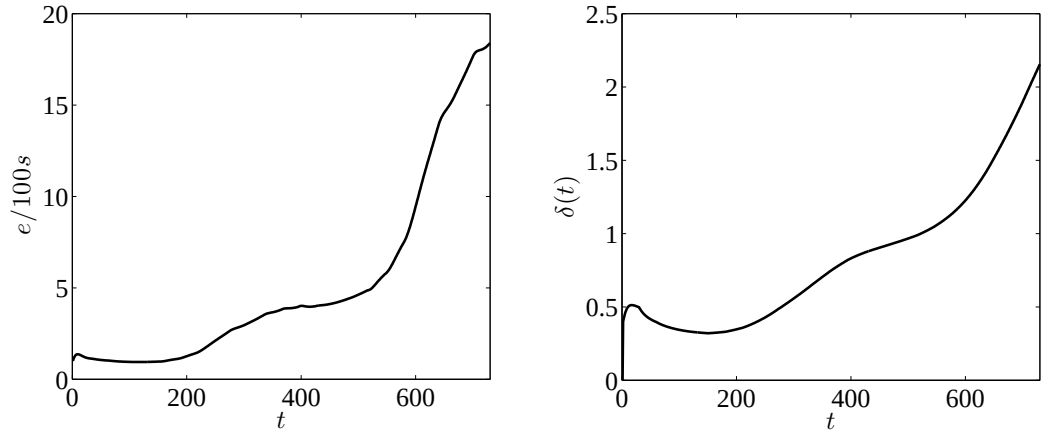


FIGURE 4.10: *Simulation results of larval populations and damage levels corresponding to data from the Sezela mill and the density-dependent mortality function (4.48).*

the mill data may have been obtained when larval levels were at a seasonal low. Infestation levels earlier in the season could have been much higher under the stressed conditions [35]. The amount of nutrition available for *E. saccharina* feeding is higher in stressed cane since less nutrition is used for growth, which results in a higher carrying capacity. The model without sterile releases, when assuming the density-dependent mortality function

$$b(t) = \frac{7}{(d^{2.5}+1)} \tag{4.49}$$

and an estimation of the average stalk length on day t in stressed cane given by

$$\ell(t+1) = \ell(t) + 0.16(24)(-1.32 + 0.15(\tau - 10)), \tag{4.50}$$

yields an average *E. saccharina* infestation of 5.7 e/100s at 13.6 months, and a percentage internodes damaged of 2.3%, which corresponds more closely to the 2010 Sezela mill data. The potential damage at 24 months, should farmers not have harvested early, is estimated by the model at 6.3% and a decrease of 10.27% in revenue per hectare (see Figure 4.11).

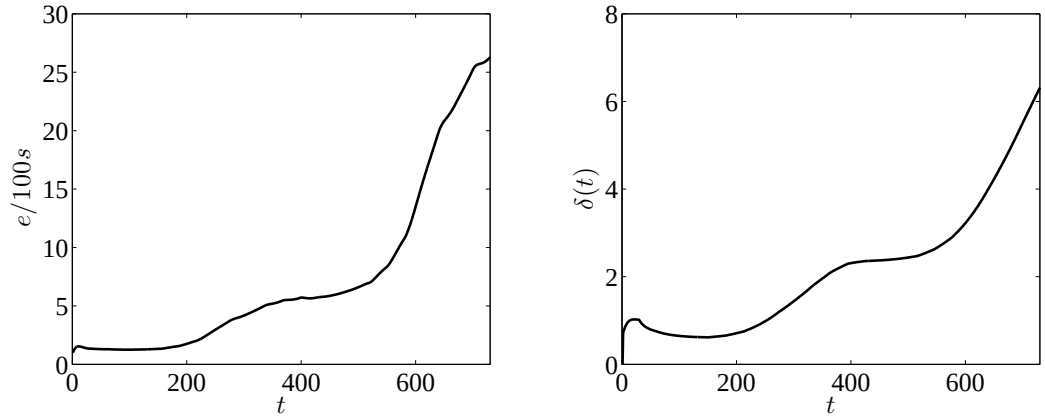


FIGURE 4.11: *Simulation results of larval populations and damage levels in stressed conditions corresponding to 2010 data from the Sezela mill and the density-dependent mortality function (4.49).*

The data obtained from the Sezela mill have been averaged data from different farms, and may not accurately represent infestation and damage levels for a specific farm. The model output

was also compared to 2009 data sets obtained from specific fields at the Eston pilot site where infestation and damage levels were monitored at least once a month during the period when the cane age was between 14 and 18 months. Data obtained from the Eston pilot site for 2009 indicates an average of 7 $e/100s$ at an average cane age of 15 months. The average percentage stalks red was measured at 6.3% [35]. The model without sterile releases, when assuming the density-dependent mortality function

$$b(t) = \frac{3}{(d^{1.1}+1)} \tag{4.51}$$

and an estimation of the average stalk length on day t in stressed cane given by (4.50) yields an average *E. saccharina* infestation of 8 e/100s and the percentage internodes damaged equal to 5%, which corresponds closely to the pilot site infestation data. However, the model seems to underestimate damage by about 20%. Data from the pilot site were obtained mainly during the months of September and October, after the winter larval peak, and may not accurately represent infestation levels experienced. This may explain why the model underestimates damage levels (infestation levels may have been higher). The potential infestation and damage at 24 months is estimated by the model at 12.2 e/100s and 8.5%, respectively. Infestation and damage data obtained during 1998 from a biological control research project performed in the Melmoth area in Kwazulu Natal included infestation levels during winter and summer months of the last few months of growth for certain fields. The model results without sterile releases, when assuming the density-dependent mortality function

$$b(t) = \frac{1.2}{(d^{1.1}+1)}, \tag{4.52}$$

compared well to infestation and damage data from the biological control site (see Figure 4.12).

In order to test whether the model underestimates damage or whether infestation levels may

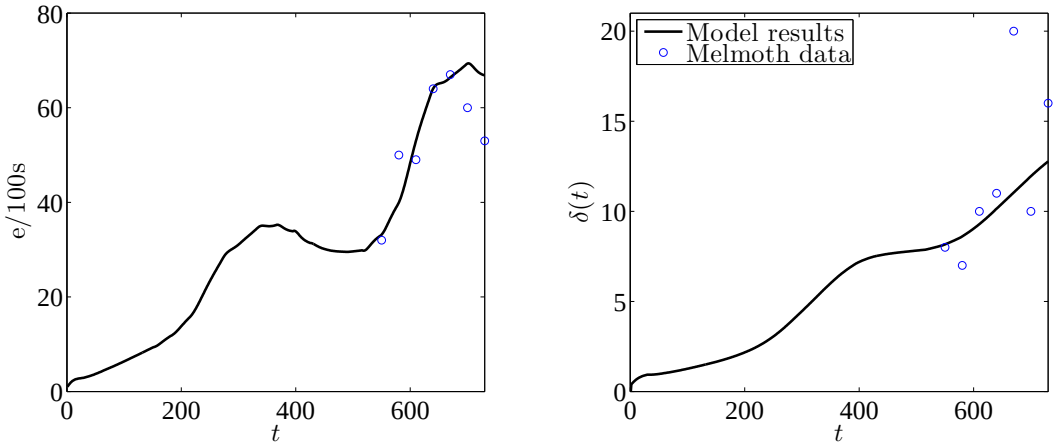


FIGURE 4.12: *Comparison of infestation and damage data obtained from the Melmoth area with simulation results.*

have been higher, infestation and corresponding damage data for every month of the crop cycle are required. Unfortunately, no such data were available during the time of this study.

If sterile moths were released, starting in the beginning of the sugarcane cycle in a scenario similar to the Sezela mill recorded infestation levels with $b(t) = \frac{7}{(d^{2.5}+1)}$, the minimum daily release ratio of sterile moths to suppress *E. saccharina* exponential growth is 0.06685 : 1. This ratio seemed to be too low compared to release ratios of other SIT projects [1, 35, 51]. However, the ratio of 0.06685 : 1 is a daily release ratio whereas most of the recorded release ratios are per

generation. If releases are daily, the released moth population increases quickly to levels where suppression is possible and no exponential growth occurs since the probability of fertilization by a sterile sperm remains higher than the probability of fertilization by a fertile sperm during the entire sugarcane cycle (see Figure 4.13). The larval population at the end of the cycle is 1.2192 e/100s with only 0.9869% of internodes damaged.

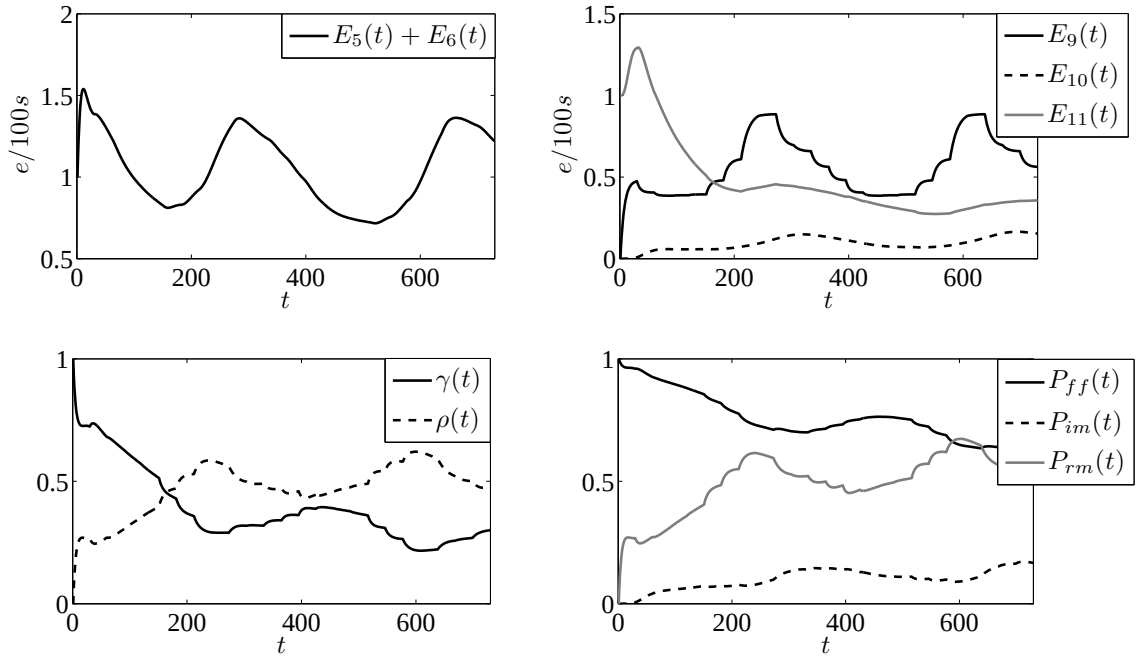


FIGURE 4.13: *Simulation results of the larval and moth populations under the influence of sterile releases together with the mating and fertilization probabilities over time. Infestation levels without sterile releases correspond to the 2010 Sezela mill data and density-dependent mortality function (4.49).*

As a result of the potential error in the estimation of $\delta(t)$ due to certain sugarcane growth factors not taken into account, the potential percentage decrease in $\delta(t)$, rather than the actual values for $\delta(t)$, are estimated for different release strategies in order to compare the effect of SIT in a certain infestation scenario. The Sezela region may have experienced more than an estimated 53% decrease in damage levels had they applied SIT. The total release cost is estimated at R4 328.80, with an estimated increase in revenue of R2 360 per hectare.

In order to estimate a more comparable release ratio with existing SIT projects, weekly rather than daily releases were also simulated. The model calculates the change in the number of released sterile moths per day via the expression

$$f_{11}(t, \underline{\mathcal{E}}) = r(t) - \mu_S(t, \tau)\mathcal{E}_{11}(t), \tag{4.53}$$

where $r(t)$ and $\mu_S(t, \tau)$ denote the daily release and mortality rates, respectively. If, however, releases are once per week with the release rate equal to zero on any other day, the mortality rate needs to be adjusted accordingly. The number of moths which die on a specific day should rather be calculated as a fraction of the number of moths present on the previous release day rather than a fraction of the moths present on the previous day. If the change in the number of released sterile moths per day is given by

$$f_{11}(t, \underline{\mathcal{E}}) = r(t) - \mu_S(t, \tau)\mathcal{E}_{11}(t_r), \tag{4.54}$$

where $\mathcal{E}_{11}(t_r)$ denotes the released moth population on the previous release day, the release ratio

necessary to suppress an *E. saccharina* infestation is estimated at 0.775 : 1, with an estimated release cost of R769.60.

The release ratio once per week also seemed to be too low compared to current SIT projects. Many ecological models, including the model described in §4.3, assume 'global' migration where the underlying assumption is that all areas within the habitat are equally connected and that individual organisms encounter one another in proportion to their average abundance across space (mean-field assumption) [38]. The model described in §4.3 assumes an even distribution of *E. saccharina* released and native populations across the entire domain during each time step. If sterile moths were to be released from a vehicle on the edge of a field (as in the current SIT release programs), this appears to be a rather unrealistic assumption, since *E. saccharina* seems to be a relatively weak flier and released sterile moths may take a few time steps to disperse to the middle of a large field [7]. The model described in §4.3 is only realistic if aerial releases are performed in such a way that a uniform distribution of released sterile moths is achieved, or if the habitat size is small enough for released sterile moths to disperse across the entire habitat in one time step. If the habitat size is too large, the suppression effect of SIT applied by means of a vehicle will take longer to realise, since released sterile moths will take a few time steps to disperse across the entire habitat so as to be able to influence all the mating probabilities. Also, in the context of a sugarcane farm, a number of sugarcane varieties may be planted on different fields, all having different ages and therefore different harvesting times. This, in turn, results in a heterogeneous environment where different *E. saccharina* subpopulations do not experience the same mortality rates. If the environment is heterogeneous, the population growth and distribution of *E. saccharina* can therefore not be described by the mean-field approximation and needs to be modelled as a function of both time and space. In order to present a more realistic model for unevenly distributed releases, or for a heterogeneous environment, a spatial dimension is included in the mean-field model described in §4.3. The spatio-temporal model is derived and considered in detail in the next chapter.

4.8 Numerical Analysis

Release strategies for different release scenarios have been obtained by means of simulations. For each release frequency, the number of released moths at each release was calculated according to the release ratio and the initial infestation (at the start of the simulation) within the domain. The initial infestation was assumed the same in all the simulations, therefore, the number of released moths per release for each frequency and release ratio was the same. Also, for each release frequency the optimal release ratio which maximises profit was obtained. The optimal release strategy $(\eta, \theta)_{opt}$ was obtained by comparing the profit obtained at the optimal release ratios for the different release frequencies. All simulations were performed for a field size of 1 ha over a time period of 24 months for cane planted in November, with an initial infestation of 0.1 e/100s and appropriate initial values for larvae, pupae and moth populations. For illustrative purposes, the cost per sterile insect (excluding labour and fuel costs) was assumed to be R0.10, and the UAV cost per application (labour and fuel) was assumed to be R5.80/ha. The application cost depends on the method of release, with a higher cost if an aircraft is used instead of an *all terrain vehicle* (ATV). The fertile proportion of the F_1 generation of released sterile males was set equal to 0.1, the residual fertility in released moths was taken as 0, the male and female competitiveness were set equal to 1 and 0.1, respectively, sperm competitiveness was taken as 1, and sterile releases was assumed to include males and females. Growing conditions were assumed ideal; therefore the average stalk length on day t is given by (4.41), with a stalk

height of approximately 1.4 m at maturation. Also, a density-dependent mortality function

$$b(t) = \frac{4}{(d^{2.5} + 1)}$$

was assumed. Simulations were performed for both a resistant ($\omega = 5$) and susceptible variety ($\omega = 8$). Infestation and damage profiles for both type of varieties are shown in Figure 4.14. After 24 months, the resistant variety is expected to yield R24 914.92/ha (comprising a loss in revenue of R2 332.55/ha) with $\delta = 5.2629$, whereas the more susceptible variety is expected to yield R19 964.16/ha (comprising a loss in revenue of R7 283.31/ha) with $\delta = 16.4332$ [84].

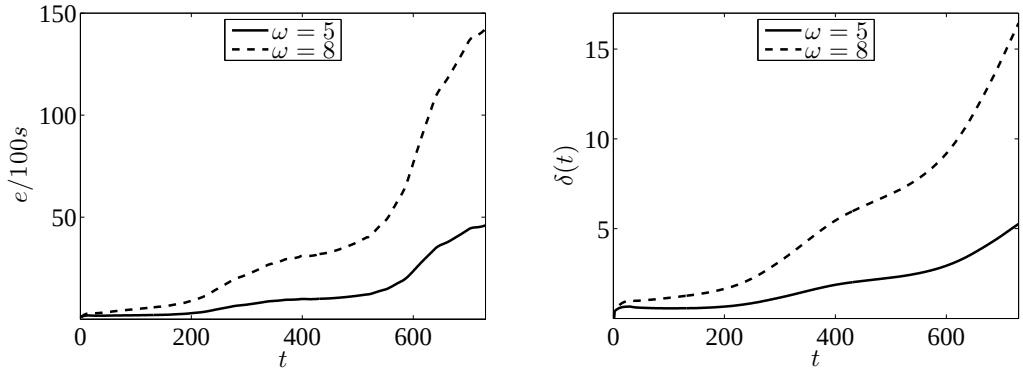


FIGURE 4.14: *Simulation results of E. saccharina larval infestation and corresponding percentage internode damage for $\omega = 5$ and $\omega = 8$.*

4.8.1 Daily releases

Suppression of *E. saccharina* below 5 e/100s with SIT releases performed on a daily basis required a minimum release ratio between 0.1 and 0.15 in the resistant cane variety, whereas suppression of *E. saccharina* in the more susceptible cane variety required a minimum release ratio between 0.3 and 0.35. For release ratios greater than 0.15 and 0.35 in the resistant and susceptible variety, respectively, the increase in revenue was only marginal (see Figure 4.15 and 4.16). The SIT release cost, however, increases linearly with an increase in the release ratio. The maximum SIT profit (P) for the susceptible variety was obtained at a release ratio of 0.362 : 1, and translates to R2 206.96. SIT releases performed on a daily basis are considered not economically viable for the resistant variety, since the SIT release cost is much higher than the expected increase in revenue. No profit was therefore obtained for the resistant variety. The release ratio which gives the smallest loss is 0.132 : 1.

4.8.2 Twice a week releases

Suppression of *E. saccharina* below 5 e/100s with SIT releases performed twice a week required a minimum release ratio between 0.2 and 0.25 in the resistant cane variety, whereas suppression of *E. saccharina* in the more susceptible cane variety required a minimum release ratio between 0.7 : 1 and 0.8 : 1. The maximum SIT profit for the resistant variety was obtained at a release ratio of 0.333 : 1, and translates to R622.33, whereas the break-even points were obtained at release ratios of 0.217 : 1 and 1.72 : 1 (see Figure 4.17). The maximum SIT profit for the susceptible variety was obtained at a release ratio of 0.913 : 1, and translates to R5 126.96, whereas the break-even points were obtained at release ratios of 0.423 : 1 and 11.51 : 1 (see Figure 4.18).

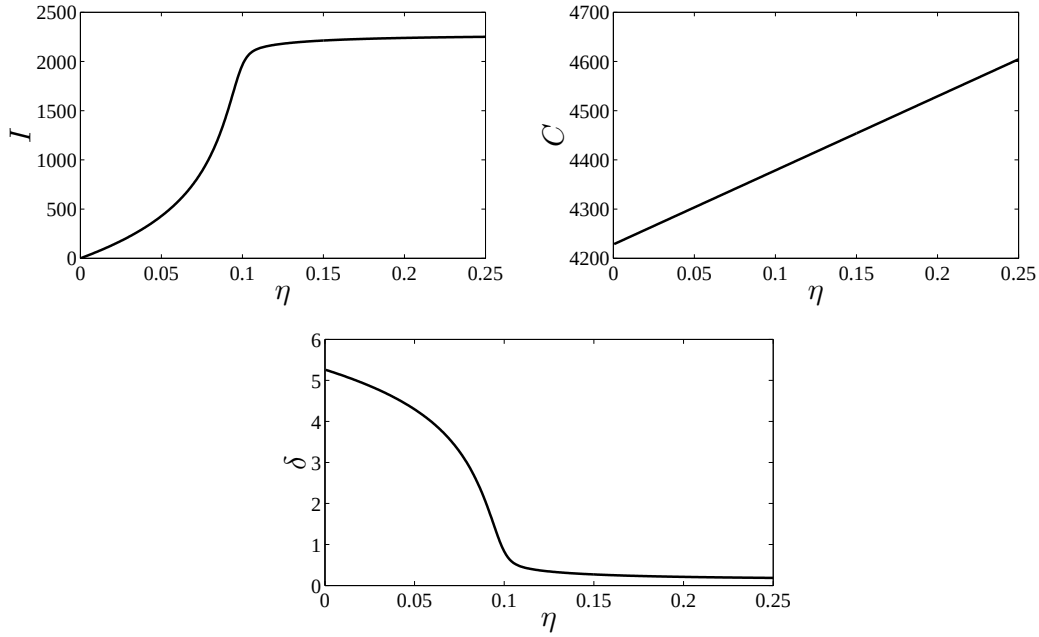


FIGURE 4.15: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 5$ *and with the release strategy varied from* $(0.0005, 1)$ *to* $(0.25, 1)$.

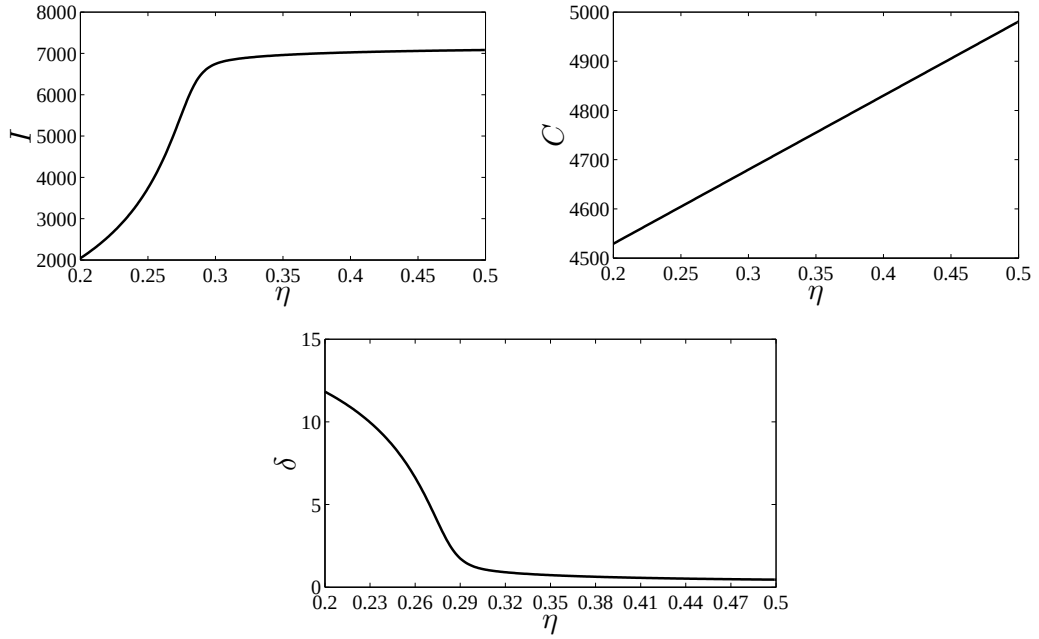


FIGURE 4.16: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 8$ *and with the release strategy varied from* $(0.2, 1)$ *to* $(0.5, 1)$.

4.8.3 Weekly releases

Suppression of *E. saccharina* below 5 e/100s with SIT releases performed once a week required a minimum release ratio between 1.15 : 1 and 1.2 : 1 in the resistant cane variety, whereas suppression of *E. saccharina* in the more susceptible cane variety required a minimum release

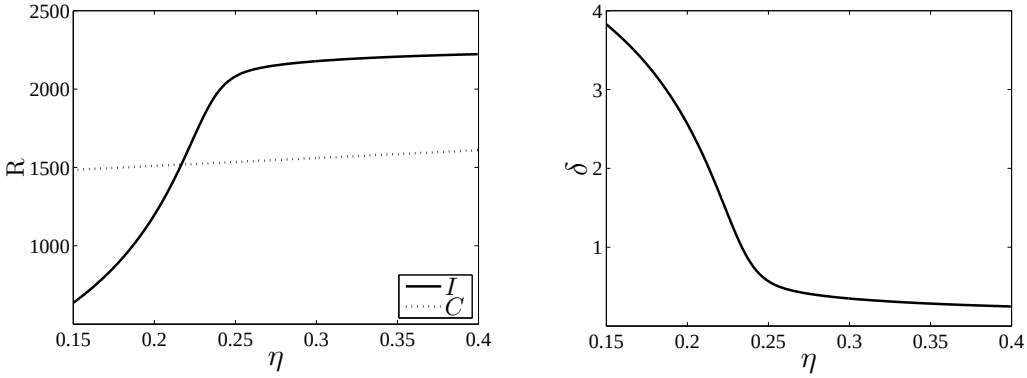


FIGURE 4.17: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 5$ *and with the release strategy varied from* $(0.15, 3)$ *to* $(0.4, 3)$.

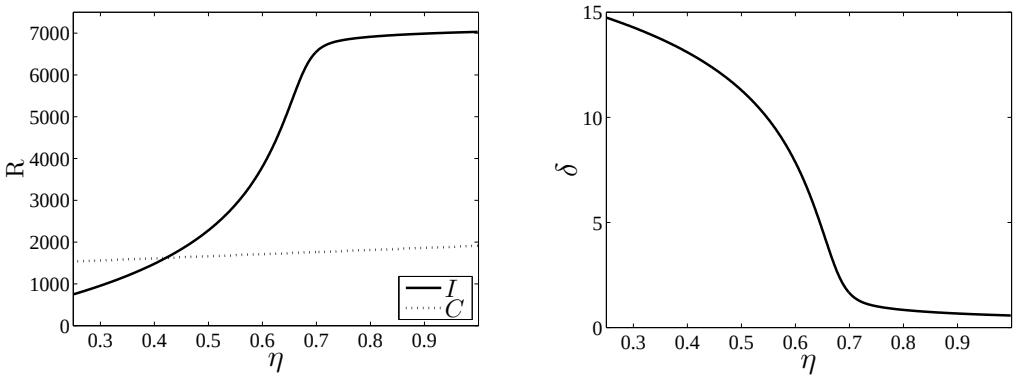


FIGURE 4.18: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 8$ *and with the release strategy varied from* $(0.25, 3)$ *to* $(1, 3)$.

ratio between 3.75 : 1 and 3.8 : 1. The maximum SIT profit for the resistant variety was obtained at a release ratio of 1.422 : 1, and translates to R1 241.20, whereas the break-even points were obtained at release ratios of 0.755 : 1 and 7.745 : 1 (see Figure 4.19). The maximum SIT profit for the susceptible variety was obtained at a release ratio of 4.287 : 1, and translates to R5 331.08, whereas the break-even points were obtained at release ratios of 1.253 : 1 and 30.52 : 1 (see Figure 4.20).

4.8.4 Two weekly releases

Suppression of *E. saccharina* below 5 e/100s with SIT releases performed once every two weeks required a minimum release ratio between 7.75 : 1 and 8.25 : 1 in the resistant cane variety, whereas suppression of *E. saccharina* below 20 $e/100s$ in the more susceptible cane variety required a minimum release ratio between 48 : 1 and 64 : 1. Suppression below 5 e/100s was not possible in the susceptible variety, even at high release ratios of 200 : 1. The maximum SIT profit for the resistant variety was obtained at a release ratio of 6.785 : 1, and translates to R793.52, whereas the break-even points were obtained at release ratios of 1.69 : 1 and 16.83 : 1 (see Figure 4.21). The maximum SIT profit for the susceptible variety was obtained at a release ratio of 22.72 : 1, and translates to R1 875.98, whereas the break-even points were obtained at release ratios of 2.32 : 1 and 51.28 : 1 (see Figure 4.22).

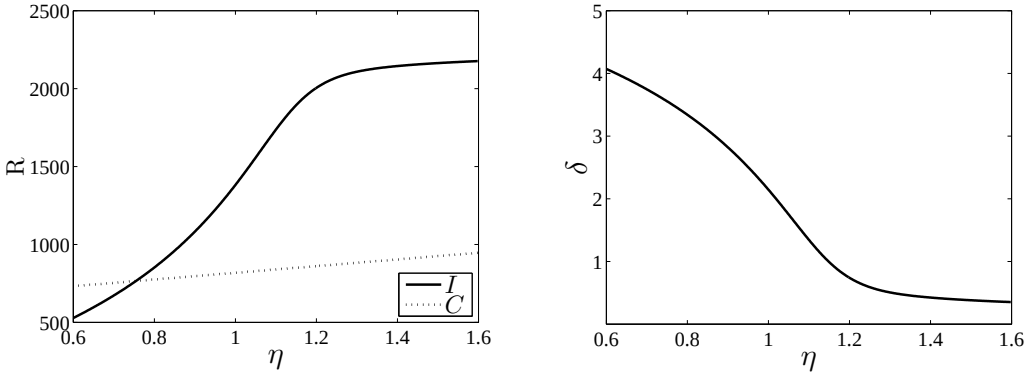


FIGURE 4.19: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 5$ *and with the release strategy varied from* $(0.6, 7)$ *to* $(1.6, 7)$.

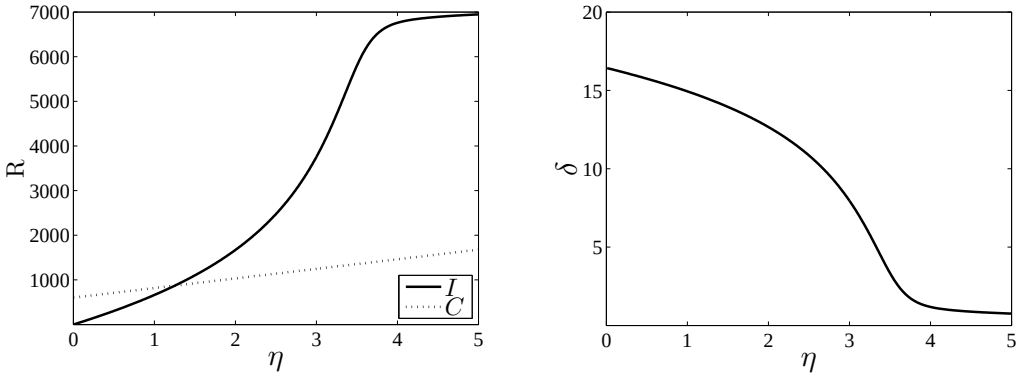


FIGURE 4.20: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 8$ *and with the release strategy varied from* $(0.01, 7)$ *to* $(5, 7)$.

4.8.5 Three weekly releases

The lifespan of an Eldana moth is approximately one week; released sterile moths therefore have more or less a week in which they have an impact on the native population. If releases were performed only once every three weeks, suppression of *E. saccharina* below 5 e/100s became difficult, as there was more time during which there were no sterile moths than when there were sterile moths present. Even at a release ratio of 1 000 : 1, suppression below 10 e/100s was not possible (see Figure 4.23). The maximum SIT profit for the resistant variety is obtained at a release ratio of 8 : 1, and translates to R151, whereas the break-even points are obtained at release ratios of 2.5 : 1 and 12.5 : 1 (see Figure 4.24). The maximum SIT profit for the susceptible variety is obtained at a release ratio of 16 : 1, and translates to R340.37, whereas the break-even points are obtained at release ratios of 3 : 1 and 33 : 1 (see Figure 4.25). If compared to the SIT profits of the other strategies, and the high infestation levels regardless of sterile insect releases, SIT releases less frequent than once every two weeks are considered not economically feasible strategies.

4.8.6 Optimal release strategy

Releases performed weekly were shown to be more cost effective compared to releases performed twice a week. The optimal aerial release strategy (for the assumed parameter values and initial infestation level) where the SIT profit P is maximised, was estimated at $(1.422, 7)$ and $(4.287, 7)$

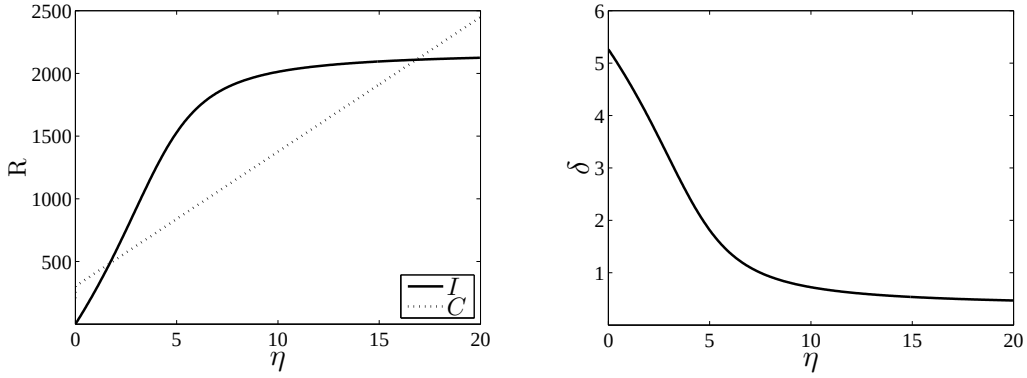


FIGURE 4.21: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 5$ *and with the release strategy varied from* $(0.01, 14)$ *to* $(20, 14)$.

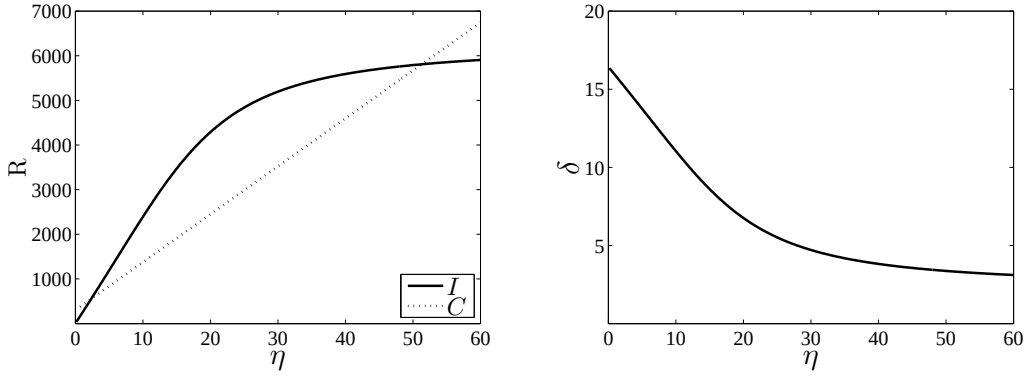
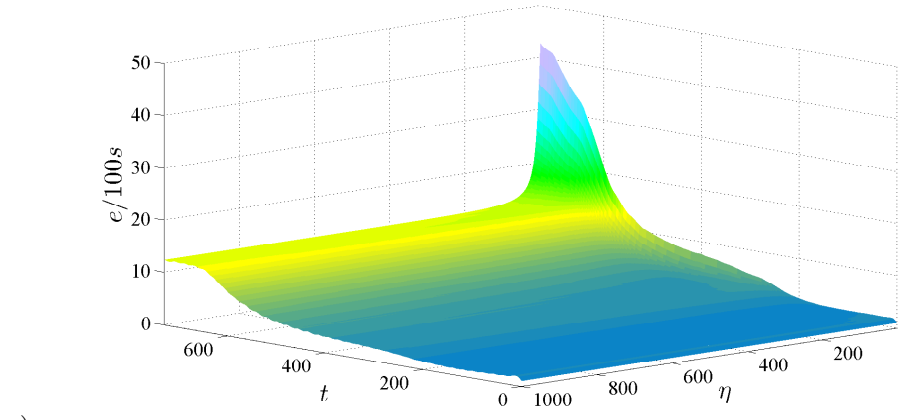


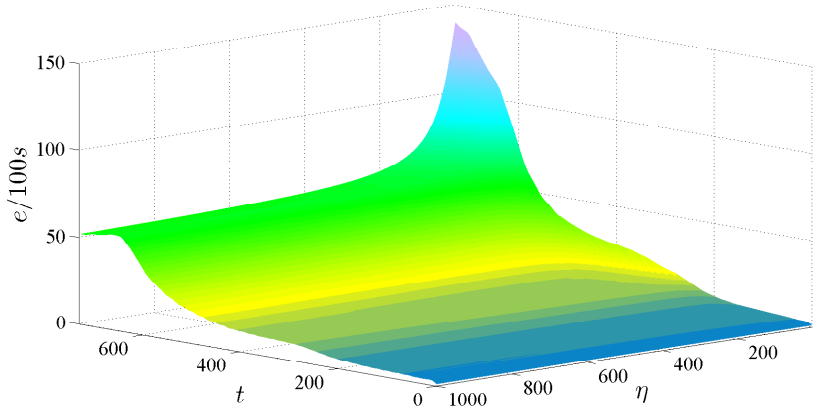
FIGURE 4.22: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 8$ *and with the release strategy varied from* $(0.01, 14)$ *to* $(80, 14)$.

for the resistant and susceptible variety, respectively. The optimal release ratios, assuming the same parameter values and initial infestation level, of cane varieties with resistance ratings between 5 and 10 are given in Table 4.6. The application cost of aerial releases may be higher than R5.80 per hectare; however, this would not change the optimal release ratio. This is easily verifiable in Figures 4.26 and 4.27, where, if the application cost increases, the graph representing C will only shift up with no change in the gradient of the graph, therefore having no effect on the optimal release ratios. If $\kappa_r \neq 0.1$, then the optimal release ratio may change due to a change in the gradient of the graph representing C. The values of C represented in Figures 4.26 and 4.27 at different release ratios (assuming an initial infestation of 0.1 e/100s) were obtained under the assumption that releases were performed twice a week or weekly over a period of two years. In areas where sugarcane cycles are less than two years, C will be half that of the values represented in Figures 4.26 and 4.27.

For cane with a similar infestation profile than the resistant and susceptible variety used in the simulations, the maximum increase in revenue was estimated R2 332.55/ha and R7 283.31/ha, respectively, and, for any economically viable strategy, this should also be the maximum cost allowed per hectare. As mentioned in §4.7, it is possible that the model underestimates δ, in which case the maximum increase in revenue may be greater than R2 332.55/ha and R7 283.31/ha, respectively. If the model underestimates δ, the optimal release ratio may change. Infestation levels, on the other hand, at different release ratios will remain the same, and hence the minimum release ratio required for suppression below 5 e/100s remains the same.



a)



b)

FIGURE 4.23: *a) E. saccharina larval infestation under the influence of sterile releases once every three weeks at different ratios with* $\omega = 5$. *The release ratio is varied from* $2:1$ *to* $1000:1$. *Suppression below* 20 *e/100s was obtained at a release ratio between* $20:1$ *and* $22:1$. *b) E. saccharina larval infestation under the influence of sterile releases once every three weeks at different ratios with* $\omega = 8$. *The release ratio is varied from* $2:1$ *to* $1000:1$. *Suppression below* 60 *e/100s is obtained at a release ratio between* $220:1$ *and* $222:1$.

4.9 Sensitivity Analysis

As mentioned in §4.7, simplifying assumptions are made in the derivation of any mathematical model in order to describe a part of a real-world process. The input parameter values and assumptions made may also be subject to many sources of uncertainty, which include errors of measurement and a partial understanding of the driving forces behind processes [80]. The model described in §4.3 assumes certain parameter values obtained from laboratory experiments, which may be different from data in actual field behaviour. For some of the parameter values, no experimental values were available at the time of writing, and certain values had to be assumed. In order to test whether the model output is reliable, it is necessary to investigate the potential changes and errors and their impacts on conclusions drawn from the model. This process is known as *sensitivity analysis* [9]. The most basic approach towards a sensitivity analysis involves perturbing a single input parameter while keeping all other parameters constant. The percentage change in the parameter is then compared to a percentage change in an output parameter in order to ascertain how robust the output is in the face of different parameter values. If the

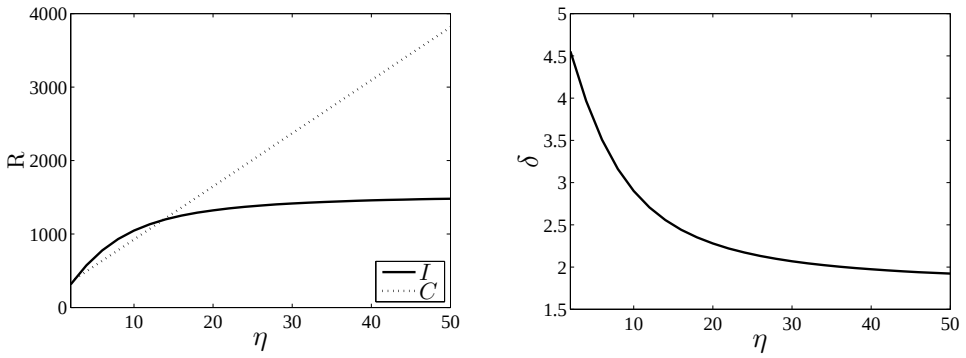


FIGURE 4.24: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 5$ *and with the release strategy varied from* $(2, 21)$ *to* $(1000, 21)$.

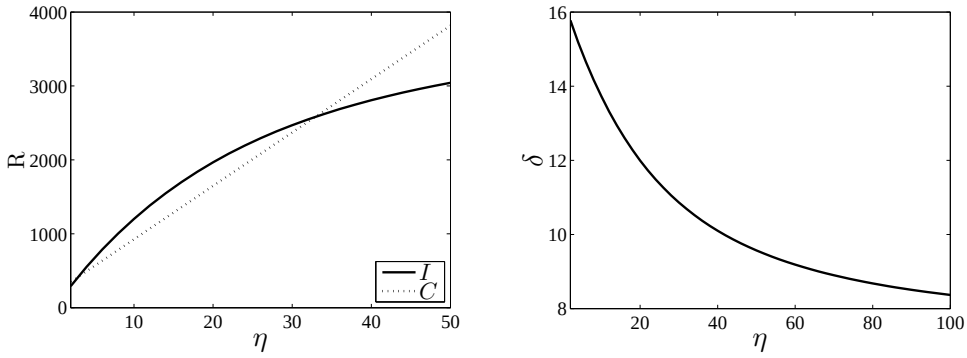


FIGURE 4.25: *The expected increase in revenue, SIT release cost and percentage internode damage for* $\omega = 8$ *and with the release strategy varied from* $(2, 21)$ *to* $(1000, 21)$.

output is insensitive to changes in parameter values, confidence in implementing the model is gained. However, if the model is sensitive to changes in parameter values, sensitivity analysis may be used to assess the significance of the risk involved in adopting a certain strategy or scenario [80]. For the purposes of decision aid, this basic approach is considered adequate [80]. A more formal and explicit use of probabilities in sensitivity analysis was therefore, and also due to a lack of knowledge about the probability distribution of most of the parameter values, excluded from the sensitivity analysis presented in this section.

4.9.1 Sensitivity of η_{opt} to changes in *E. saccharina* parameters

The sensitivity of the optimal release ratio to changes in sterile-specific parameters, as well as growth, maturation and mortality parameters, was tested by perturbing the various parameters by a certain percentage, and then finding the optimal release ratio for the new set of parameter values. From Figure 4.28 the optimal release ratio appears to be relatively insensitive to changes in the parameters α_E, μ_P, β, μ_M, z, c_f, α_P, κ_ℓ. The optimal release ratio is the most sensitive

ω	5	6	7	8	9
η_{opt}	1.422	1.974	2.836	4.287	7.029

TABLE 4.6: *Optimal release ratios for cane varieties with different resistance ratings.*

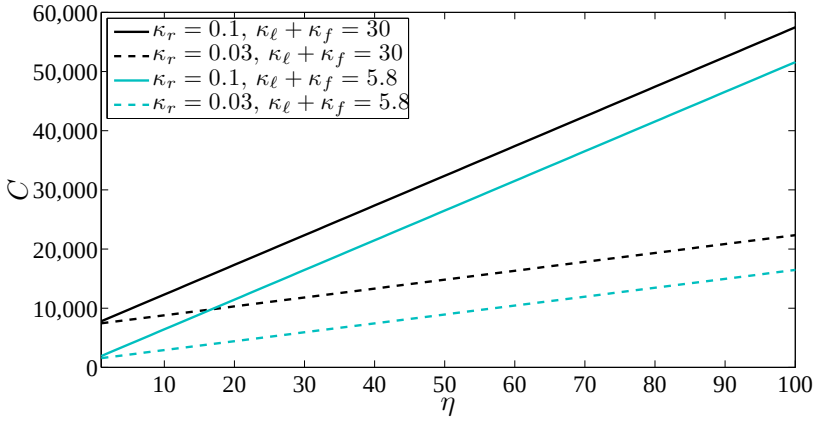


FIGURE 4.26: *Comparison between estimated values of C at different release ratios with aerial releases performed twice a week on a 1 hectare field over a period of 24 months.*

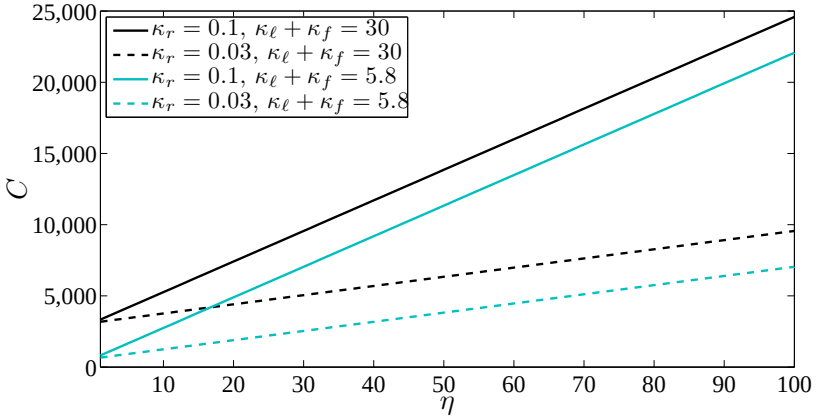


FIGURE 4.27: *Comparison between estimated values of C at different release ratios with aerial releases performed weekly on a 1 hectare field over a period of 24 months.*

to changes in λ_f, μ_{L_1}, μ_{L_2}, α_{L_1}, α_{L_2}, c_m, m and y. The average elasticities[4] of η_{opt} with respect to changes in the various parameters are given in Table 4.7. The optimal release ratio does not appear to be very sensitive to changes in the initial infestation level (see Table 4.8) or the maximum number of matings per moth (see Tables 4.9 and 4.10). In the case that the model underestimates damage levels, η_{opt} is not too sensitive to changes in damage levels (the elasticity of η_{opt} with respect to changes in σ is 0.134).

4.9.2 Sensitivity of max(P) to changes in *E. saccharina* parameters

The sensitivity of the maximum SIT profit with respect to changes in sterile specific parameters, as well as growth, maturation and mortality parameters, was tested by perturbing the various parameters by a certain percentage, and then finding the maximum SIT profit (the profit obtained at the optimal release ratio) for the new set of parameter values. From Figure 4.29 max(P) appears to be relatively insensitive to changes in the parameters λ_s, μ_E, μ_P, β, z, c_f, α_P and α_E. The maximum SIT profit is the most sensitive to changes in α_{L_2}, λ_f, κ_ℓ, κ_f, μ_{L_1},

[4]The elasticity of a dependent variable is a measure of the percentage change in the variable for every one percentage point change in an independent variable (parameter).

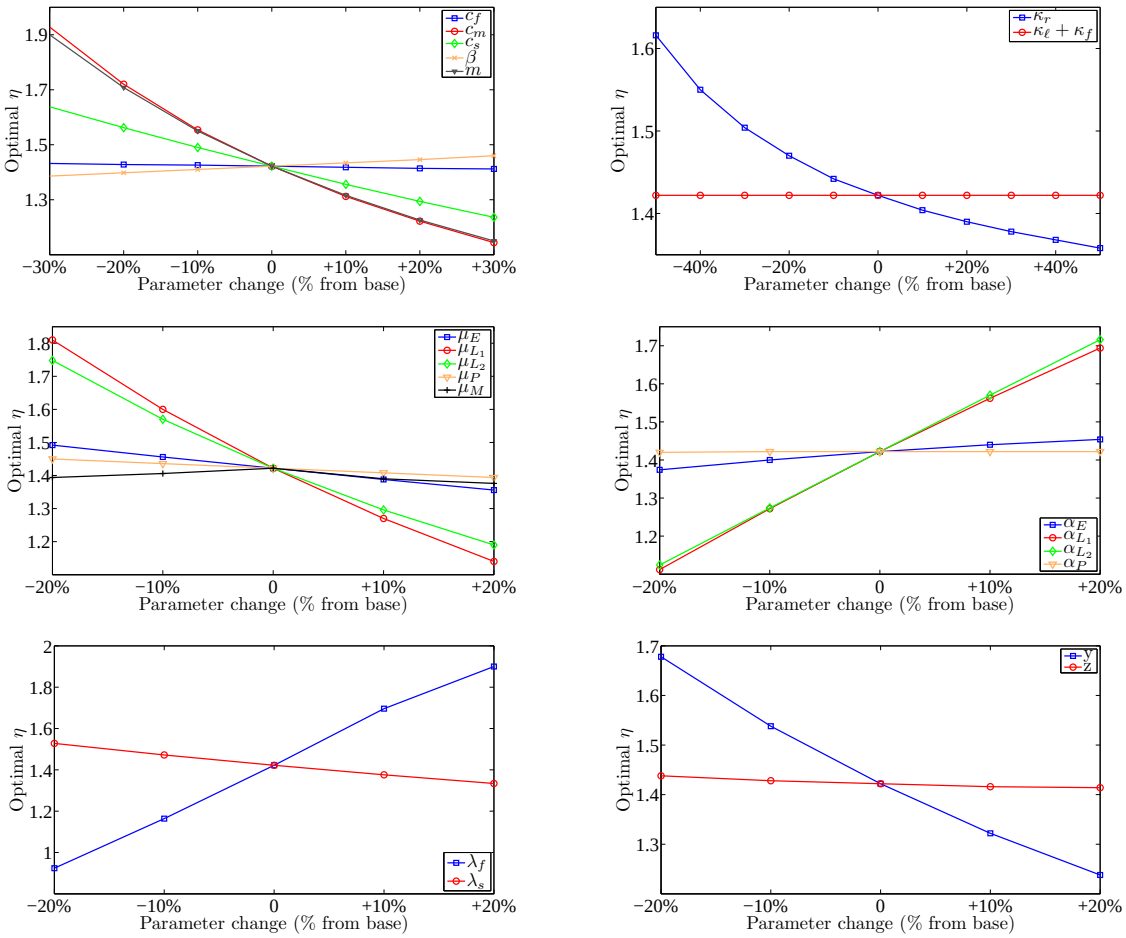


FIGURE 4.28: *The sensitivity of the optimal release ratio to changes in various parameters.*

α_{L_1}, μ_{L_2}, μ_M, c_m, m, y and κ_r. The average elasticities of $\max(P)$ with respect to changes in various parameters are given in Table 4.7. The maximum SIT profit is very sensitive to changes in the initial infestation level (see Figure 4.30 and Table 4.8) — for a specific release ratio, the number of moths released is larger for higher initial infestation levels, thereby increasing the release cost and decreasing the SIT profit. In order to maximise SIT profit, care should therefore be taken to apply SIT when initial infestation levels are at a seasonal low, or to apply SIT in combination with other control measures, as mentioned in §2.3. The maximum SIT profit is rather insensitive to changes in the maximum number of matings per moth (see Tables 4.9 and 4.10). In the case that the model underestimates damage levels, $\max(P)$ is not too sensitive to changes in damage levels (the elasticity of $\max(P)$ with respect to changes in σ is -0.148).

4.9.3 Sensitivity of δ to changes in *E. saccharina* parameters

The sensitivity of δ with respect to changes in sterile specific parameters, as well as growth, maturation and mortality parameters, was tested by perturbing the various parameters by a certain percentage (but keeping the release ratio constant at 1.422), and then finding δ for the new set of parameter values. From Figure 4.31, δ appears to be relatively insensitive to changes in the parameters β, z, c_f, α_P, κ_r, κ_ℓ and κ_f. The percentage damage is the most sensitive to changes in λ_f, μ_{L_1}, μ_{L_2}, α_{L_1}, α_{L_2} (which correspond to the sensitivity analysis of the model

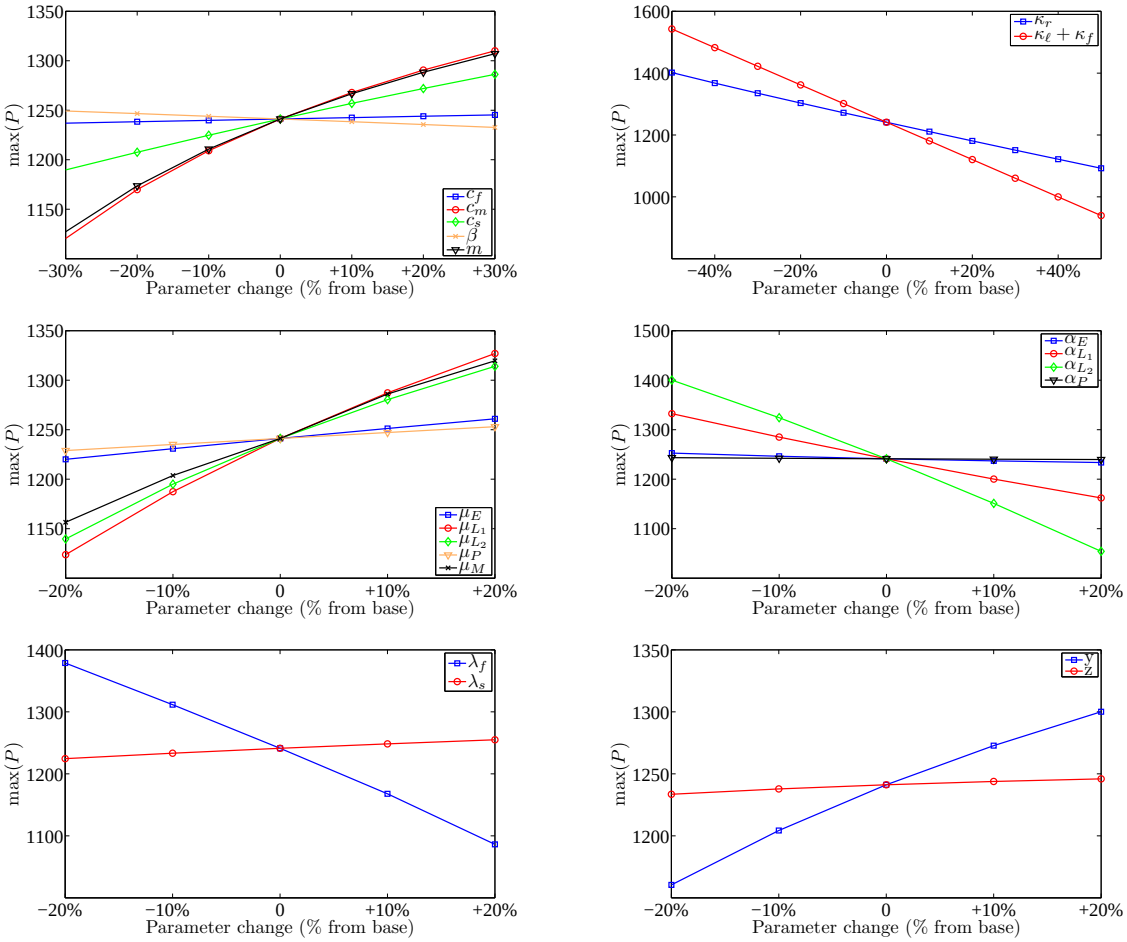


FIGURE 4.29: *The sensitivity of the maximum profit to changes in various parameters.*

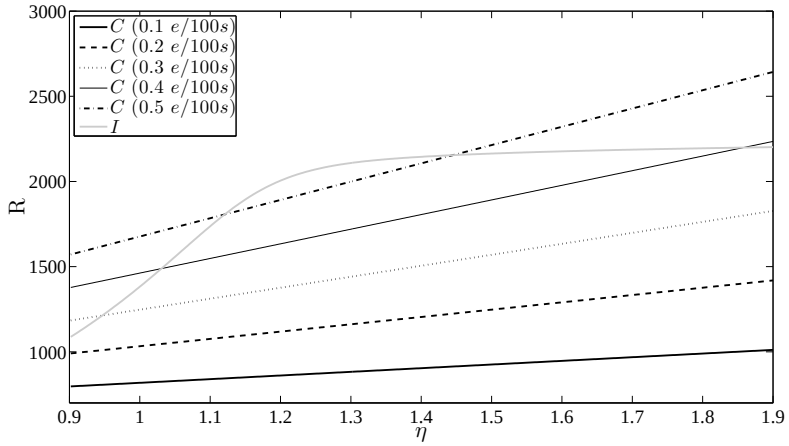


FIGURE 4.30: *Sterile release costs for different initial values are compared. As the initial infestation increases, P decreases.*

proposed by Horton [52]), c_m, m, y, c_s and σ. Also, δ is much more sensitive when decreasing the values of c_m, c_s, m, μ_{L_1}, μ_{L_2} and y than when these parameter values are increased, and when α_{L_1}, α_{L_2} and λ_f are increased than when these parameter values are decreased. This may be understood in the light of the graph representing δ in Figure 4.19 — when release

ratios are less than η_{opt}, the slope is much higher than when release ratios are more than η_{opt}, indicating that δ is much more sensitive to a decrease in η (increase in infestation) around η_{opt} than to an increase in η around η_{opt}. Decreasing c_m, c_s, m, μ_{L_1}, μ_{L_2} and y result in higher infestation levels, whereas increasing α_{L_1}, α_{L_2} and λ_f also result in higher infestation levels which is equivalent to the effect of a smaller release ratio. The average elasticities of δ with respect to changes in various parameters are given in Table 4.7. Elasticities are given for δ when $\eta = \eta_{opt}$ and $\eta > \eta_{opt}$. The damage level δ becomes less sensitive to all parameters when $\eta > \eta_{opt}$, which is as expected when compared to Figure 4.19. The percentage damage δ is insensitive to changes in the initial infestation level (see Table 4.8) which is also expected, since non-dimensional variables were used. The percentage damage is also insensitive to changes in the maximum number of matings per female and not too sensitive to changes in the maximum number of matings per male (see Tables 4.9 and 4.10).

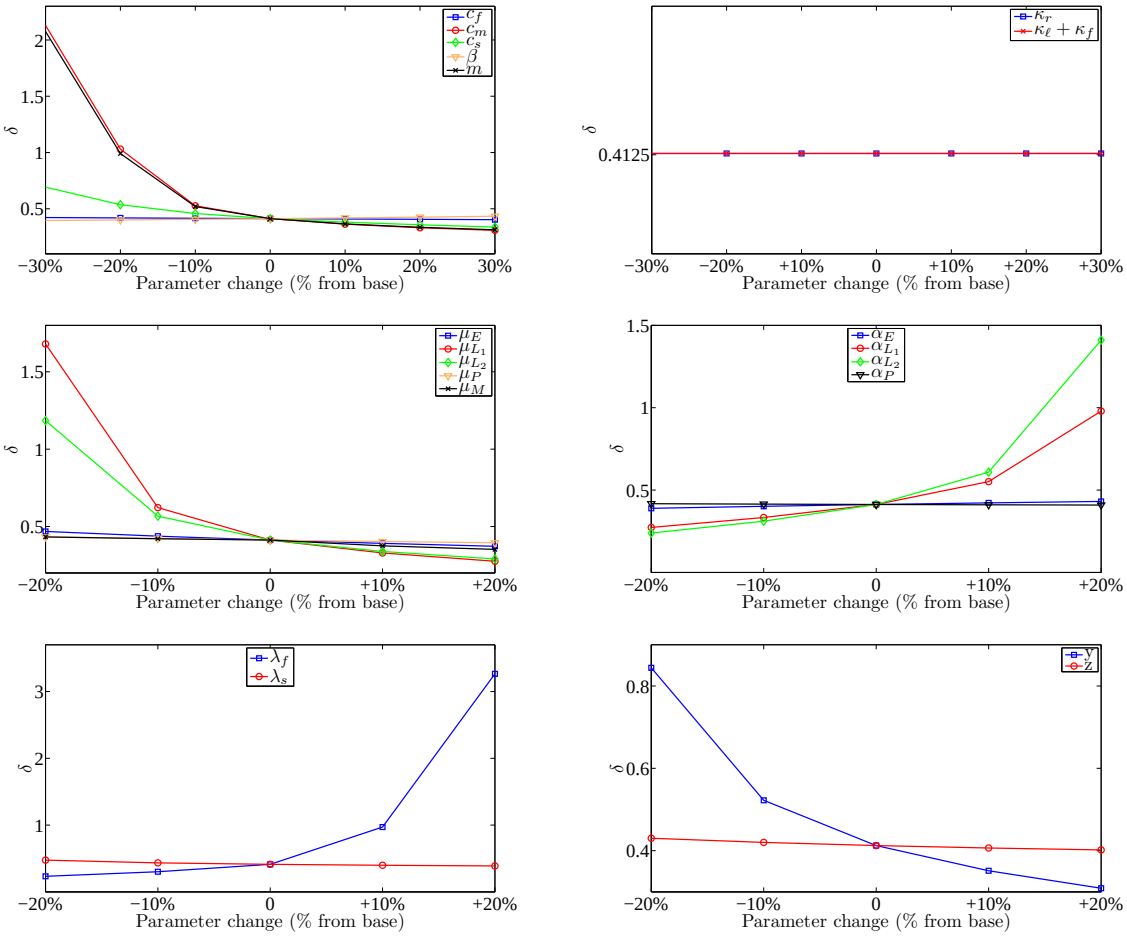


FIGURE 4.31: *The sensitivity of the percentage damage δ with respect to percentage changes in various parameters when the release ratio is kept constant at η_{opt}.*

4.9.4 Comparison between η_{opt}, max(P) and δ

From Table 4.7 it may be seen that δ around η_{opt} is the most sensitive output parameter compared to the elasticities of η_{opt} and max(P). The maximum SIT profit is the least sensitive to changes in the parameters compared to η_{opt} and δ. The elasticities of δ when $\eta = 1.422$

compared to when $\eta = 1.8$ indicates that δ becomes less sensitive at larger release ratios. If the objective is to maximise profit together with minimising risk[5] rather than only maximising profit, it may therefore be better to choose a larger value for η (where δ is less sensitive) within the profit range than to choose η_{opt} where $\max(P)$ is obtained and where δ is extremely sensitive to changes in some of the parameters. The profit estimated at $\eta = 1.8$ is R1205.08 (see Table 4.8) which is only 3% less than the profit estimated at $\eta = 1.422$. Since all of the output parameters (η_{opt}, $\max(P)$ and δ) are relatively insensitive to changes in c_f and sensitive to changes in c_m and m, released sterile males may have a much more significant impact on infestation and damage levels than released sterile females. This corresponds with the large-scale field comparison between males-only and bisexual sterile fly releases in Guatemala [89]. Releasing only sterile males instead of both males and females is therefore considered a better (and effective) strategy. The optimal release ratio, maximum SIT profit and δ were also estimated for releases starting at different crop ages (see Table 4.11). The profit was more than R1 000 if releases commenced between 0 and 5 months, with $\delta < 1$. Releases commenced at a crop age of more than 5 months resulted in increased damage levels, with the profit decreasing at a higher rate for each month older at which releases commenced (see Figure 4.32). It is therefore not recommended to commence releases at a crop age older than 5 months.

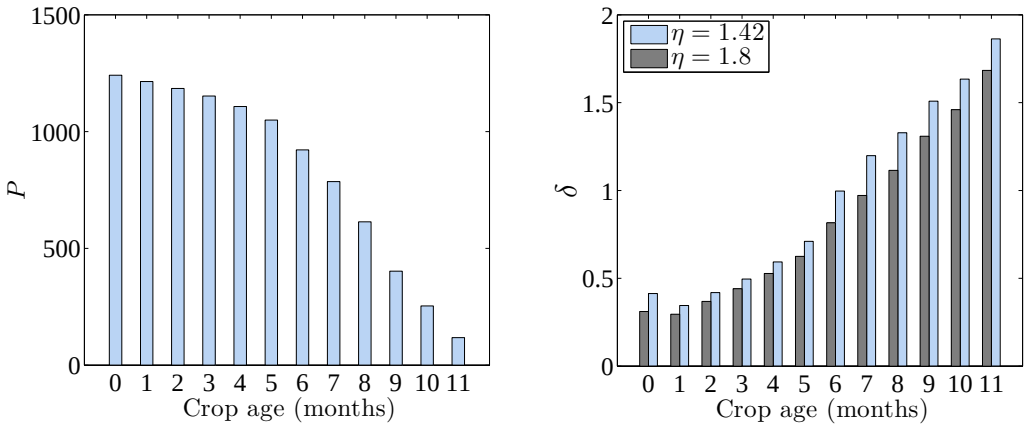


FIGURE 4.32: *SIT profit and damage levels for releases commenced at different crop ages.*

4.10 Chapter Summary

A detailed description of the *E. saccharina* population growth model and interaction with sterile released moths was presented in §4.3, along with the assumptions made (in §4.2) in order to derive the model, which forms the basis for the spatio-temporal model presented in the next chapter. A description of the parameters incorporated into the model, namely the growth rate, the stage-specific mortality rates, the density-dependent mortality rate, the stage-specific maturation rates and the SIT parameters, was also given in §4.4 together with the derivation of the fertilization probabilities γ and ρ. In contrast with previous SIT models which consider only the male mating probabilities, the fertilization probabilities in the model of §4.3 include both the probability of mating with a certain type of male (fertile or sterile) and mating with a certain type of female. In order to compare the effect of different sterile release strategies, model output parameters were defined in §4.5 which include the cost of a release strategy, the crop damage index and the increase in revenue expected from different strategies. In §4.6, the model

[5]In the context of this dissertation risk may be interpreted as higher infestation and damage levels than expected.

Parameter	Elasticity of η_{opt}	Elasticity of max(P)	Elasticity of δ when $\eta = 1.422$	Elasticity of δ when $\eta = 1.8$
λ_f	1.793	-0.584	13.245	3.106
μ_{L_1}	-1.169	0.406	-6.031	-2.018
α_{L_2}	1.041	-0.697	5.353	2.251
α_{L_1}	1.021	-0.342	3.46	1.514
μ_{L_2}	-0.972	0.348	-4.089	-1.715
c_m	-0.882	0.245	-4.524	1.155
m	-0.85	0.233	-4.319	-1.044
y	-0.767	0.279	-2.659	-1.353
c_s	-0.471	0.13	-1.145	-0.495
λ_s	-0.339	0.061	-0.481	-0.101
μ_E	-0.239	0.082	-0.571	-0.376
κ_r	-0.141	-0.246	0	0
α_E	0.141	-0.038	0.253	0.121
σ	0.134	-0.148	1	1
μ_P	-0.098	0.049	-0.233	-0.148
β	0.085	-0.022	0.152	0.078
μ_M	-0.044	0.33	-0.521	-0.281
z	-0.042	0.025	-0.168	-0.143
c_f	-0.025	0.011	-0.076	-0.07
α_P	0.002	-0.007	-0.049	-0.086
$\kappa_\ell + \kappa_f$	0	-0.489	0	0

TABLE 4.7: *Average elasticities of η_{opt}, max(P) and δ.*

Initial infestation	η_{opt}	max(P)	δ	Profit range of η	Profit when $\eta = 1.8$
0.1 $e/100s$	1.422	R1 241.19	0.4125	$[0.755; 7.745]$	R1 205.08
0.2 $e/100s$	1.326	R948.45	0.4125	$[0.855; 3.383]$	R818.61
0.3 $e/100s$	1.286	R668.41	0.4125	$[0.943; 2.522]$	432.14
0.4 $e/100s$	1.262	R394.99	0.4125	$[1.03; 1.857]$	R45.67
0.5 $e/100s$	1.242	R126.24	0.4125	$[1.12; 1.445]$	-R340.80

TABLE 4.8: *Changes in η_{opt}, max(P) and δ for various initial infestation levels. The range of η for which an SIT profit is obtained is also given, together with the profit estimated when $\eta = 1.8$.*

A	η_{opt}	max(P)	δ
1	1.422	R1 241.19	0.4125
2	1.422	R1 241.19	0.4125
3	1.422	R1 241.19	0.4125

TABLE 4.9: *Changes in η_{opt}, max(P) and δ for various number of matings per female.*

B	η_{opt}	max(P)	δ
1	1.164	R1 319.44	0.361
2	1.29	R1 282.00	0.3844
3	1.356	R1 261.77	0.3981
4	1.39	R1 251.39	0.405
5	1.414	R1 243.36	0.4115
6	1.422	R1 241.19	0.4125

TABLE 4.10: *Changes in η_{opt}, max(P) and δ for various numbers of matings per male.*

Crop age in months	η_{opt}	max(P)	δ when $\eta = 1.422$	δ when $\eta = 1.8$
0	1.42	R1 241	0.4135	0.3109
1	1.02	R1 214	0.3451	0.2957
2	1.02	R1 185	0.4189	0.3688
3	1.08	R1 152	0.4957	0.4411
4	1.16	R1 107	0.5934	0.5278
5	1.26	R1 050	0.7104	0.6248
6	1.44	R922	0.9966	0.8162
7	1.46	R786	1.1984	0.9714
8	1.34	R614	1.3283	1.1145

TABLE 4.11: *Changes in η_{opt}, max(P) and δ for releases commencing at different crop ages.*

implementation in MATLAB was verified by demonstrating expected model responses to changes in the temperature, crop variety, competitiveness of released moths and their sperm, fertility of the F_1 generation, residual fertility in the released moths and the release rate. The model was also validated in §4.7 by means of data sets obtained from the Sezela mill, the pilot site near Eston and previous experience with respect to sterile release ratios. The optimal release strategy for an assumed parameter set was obtained by means of a numerical analysis. Results of the numerical analysis are given in §4.8. A sensitivity analyses was also performed in §4.9 in order to ascertain the robustness of the optimal strategy (in terms of profit) with respect to different parameter values. The sensitivity analysis indicated that δ is very sensitive around η_{opt}. A good strategy (in terms of both profit and risk) may therefore be where $\eta > \eta_{opt}$, but still within the profit range of η, and where δ is less sensitive to changes in parameters. The optimal strategy and value of δ were found to be much more sensitive to changes in c_m than to changes in c_f, indicating that males have a much more significant impact on suppression than females. It may therefore be advisable to only release males. The sensitivity of the optimal release ratio, maximum SIT profit and value of δ were also tested by changing the crop age at which sterile releases were started. A crop age between 0 and 5 months was found to be better in terms of profit and damage levels compared to releases commenced in more mature cane.

CHAPTER 5

Spatio-temporal model

Contents

> *"... all models are approximations. Essentially, all models are wrong, but some are useful. However, the approximate nature of the model must always be borne in mind ..."*
>
> — George E.P. Box

In this chapter a detailed description of the *E. saccharina* model in a spatially and temporally variable environment is presented. The mean-field model of Chapter 4 is extended to a spatially explicit model with local dispersal between neighbouring habitats in order to investigate the effect of dispersal on SIT. A purely diffusion-based dispersal is assumed in the spatial model. After a brief description of the general modelling approach in §5.1 and the model assumptions made in §5.2, the spatio-temporal model is derived in §5.3. The model with diffusive dispersal comprises a discrete reaction-diffusion system. Zero-flux Neumann boundary conditions are assumed in the model with initial values obtained from simulations of the mean-field model of Chapter 4. In §5.4 the diffusion coefficients, release methods and the changes in parameters according to a heterogeneous environment are discussed. In §5.6, simulations are performed in order to verify whether the implementation of the model represents a correct representation of the logic contained in the mathematical description of the model. The model implementation responds as expected to changes in all parameters, thereby verifying the model. Numerical results of the model for different release methods are presented in §5.7. The model is also validated in §5.8 by means of data obtained from similar SIT projects. The chapter closes with a chapter summary in §5.10.

5.1 Description of the model

The *E. saccharina* population growth model for a spatially and temporally variable environment is derived in order to describe the spatial dynamics of a set of interacting *E. saccharina* subpopulations under the influence of a release of fully sterile females and semi-sterile males on an isolated and bounded spatial domain.

As mentioned in Chapter 4, the mean-field model described in §4.3 is not realistic in the context of a sugarcane farm comprising a heterogeneous environment, and it is also not realistic in the context of sterile releases from a vehicle driven along the edges of the fields. The usual low mobility of *E. saccharina* (only moths are able to disperse over longer distances, with moths having been observed to remain close to their emergence sites in most cases) results in the migration and colonization of migrants which are local processes in space. In this case, the distribution of *E. saccharina* can therefore not be described by the mean-field approximation — a spatially explicit model is required.

The spatial domain, within the context of this chapter, is assumed to be an isolated set of adjacent sugarcane fields surrounded by land uses not corresponding to possible habitats for *E. saccharina*. The set of sugarcane fields is divided into discrete patches of sugarcane, each patch having the same number of sugarcane stalks and being small enough to adopt the mean-field approximation within a single patch. This patchy environment is modelled as a two-dimensional arena in which *E. saccharina* subpopulations are distributed amongst a square grid of patches with subpopulations connected by dispersing individuals. The dynamics of each subpopulation are modelled by assuming the mean-field model described in Chapter 4 as reaction terms, whereas the dynamics among subpopulations (dispersal of individuals between neigbouring patches) are modelled by assuming the discretized Laplacian operator for the purpose of diffusion. The model with diffusive dispersal therefore consists of a spatially and temporally discrete reaction-diffusion system with constant diffusion coefficients. Dispersal will only occur between neighbouring patches within the spatial domain with no dispersal outside the domain as a result of the assumed land uses surrounding the set of sugarcane fields; therefore, zero-flux Neumann boundary conditions are assumed in the model.

During each day, a certain proportion of adult moths are assumed to leave the patch in which they emerged or from where they have been released, and colonize neighbouring patches within their flight range, provided that moth densities in neighbouring patches are more favourable, while the remainder stay behind to reproduce in their original patch. Dispersal may be more likely as a result of individuals searching for possible mates after remaining unmated after their first or second attempt, or as a result of females searching for more favourable oviposition sites [5]. In the case of individuals searching for possible mates, dispersal is more likely from lower density patches to higher density patches (concentrating), whereas dispersal of females searching for oviposition sites is more likely from higher density to lower density patches (spreading).

5.2 Model assumptions

The following model assumptions are made:

1. *Mean-field.* Moths are assumed to be able to disperse uniformly across an area of 25 m^2 within one time-step (a day). The mean-field assumption is therefore assumed realistic for a habitat size of 25 m^2.

2. *Population growth.* Within each patch of size not greater than 25 m^2 in the spatial domain, population growth is described via the mean-field model in Chapter 4. Growth, maturation, mortality and sterile insect specific parameters are assumed to be functions of time and temperature as described in §4.4.

3. *Mortality.* The mortality rates of larval populations inside and outside the stalks are assumed to depend on the cane variety within the specific habitat patch [52]. Larval mortality rates are therefore functions of time, temperature and space.

4. *Sterile releases.* Releases of sterile moths are assumed to occur at a constant rate over the release period, with releases performed by means of an aircraft, or an ATV. For releases from an aircraft, released sterile moths are assumed to be gaussian distributed in patches between the flight paths. For releases from an ATV, released sterile moths are assumed to be either uniformly distributed along the release lanes, or uniformly distributed across discrete patches along the release lanes.

5. *Dispersal.* At the time of this study, not much was known about the dispersal patterns of individual *E. saccharina* moths [35]. In the absence of dispersal information, the simplest assumption for dispersal is to assume that individuals follow a random walk. Moths are therefore assumed to disperse randomly in any direction to neighbouring patches without any directive movement. The assumption is only reasonable if individual moths have short-term memories, no large-scale knowledge of the landscape and if spatial heterogeneity occurs on a larger scale than behavioral mechanisms [79]. Moths have also been observed to be active mostly during the night [35, 73]; therefore dispersal is assumed to occur only during the night.

6. *Spatial heterogeneity.* The spatial domain is considered heterogeneous if it consists of a number of sugarcane fields containing cane of different varieties and ages. In the case of a spatial domain consisting of only one sugarcane field, a homogenous environment is assumed.

7. *Isolated domain.* The spatial domain is assumed to be isolated, with no other natural habitat surrounding the domain. Dispersal is therefore assumed to be only within the domain, with no migrants leaving the domain.

8. *Initial conditions.* In order to solve the model, a certain initial fertile egg population $e_1(\underline{\xi})$, initial larval population outside the stalks $e_3(\underline{\xi})$, initial larval population inside the stalks $e_5(\underline{\xi})$, initial pupal population $e_7(\underline{\xi})$, initial fertile moth population $e_9(\underline{\xi})$ and an initial released sterile population $e_{11}(\underline{\xi})$ have to be specified within each habitat patch, where $\underline{\xi}$ denotes a position vector within the patch. Initial populations are assumed to be distributed uniformly across the entire domain.

5.3 Model formulation

As mentioned in §5.2, the spatially adjusted model presented in this chapter assumes that individual moths follow a pure random walk. Assuming that the movements consist of a sequence of small steps, a good approximation to these random walks is a pure diffusion process. During each time-step, a proportion of moths disperse randomly to neighbouring habitat sites. Longer range dispersal can only occur through repetition of these short range movements over multiple time-steps. Following the notation in [106], consider the eleven populations of an *E. saccharina*

population introduced in Chapter 4 within a closed, simply connected, 2-dimensional spatial domain $\mathcal{S}$, which, in the context of this chapter, is assumed to be a set of adjacent sugarcane fields. Let $E_1(\underline{\xi},t)$, $E_2(\underline{\xi},t)$, $E_3(\underline{\xi},t)$, $E_4(\underline{\xi},t)$, $E_5(\underline{\xi},t)$, $E_6(\underline{\xi},t)$, $E_7(\underline{\xi},t)$, $E_8(\underline{\xi},t)$, $E_9(\underline{\xi},t)$, $E_{10}(\underline{\xi},t)$ and $E_{11}(\underline{\xi},t)$ denote the population density of the fertile egg population, the inherited sterile egg population, the fertile larval population outside the stalk, the inherited sterile larval population outside the stalk, the fertile larval population inside the stalk, the inherited sterile larval population inside the stalk, the fertile pupal population, the inherited sterile pupal population, the fertile moth population, the inherited sterile moth population and the released sterile moth population at position $\underline{\xi} = [\xi_1, \xi_2]^T \in \mathcal{S}$ and at time $t \in [0, \infty)$, respectively. Define $\underline{E}(\underline{\xi},t) = [E_1(\underline{\xi},t), \ldots, E_{11}(\underline{\xi},t)]^T$.

Furthermore, assume that the change of the population density of the i-th moth population (that is, for $i = 9, 10, 11$) per time unit is equal to the dispersal of the i-th population to and from adjacent habitat sites together with the amount of the i-th population created per time unit within the site. The change of the population density of all other populations per time unit at a certain position is assumed equal to the amount created per time unit, with no dispersal occurring. The diffusion matrix, $\mathbf{D}(\underline{\xi})$, therefore has entries 0 for all types of populations, except for moths. That is, $\mathbf{D}(\underline{\xi}) = \text{diag}\,\{0,0,0,0,0,0,0,0,0,d(\underline{\xi}),d(\underline{\xi}),d(\underline{\xi})\}$, where the diffusion coefficient $d(\underline{\xi})$ is a measure of how effectively moths disperse between habitat sites at position $\underline{\xi} = [\xi_1, \xi_2]^T$. Under the assumption that moths disperse randomly in any direction without any directive movement, the diffusion coefficient is constant across the entire domain and does not depend on the position $\underline{\xi}$ in the domain. However, the model is derived in such a way that it is applicable to both scenarios with constant or with variable diffusion coefficients.

As shown in [106] the population vector $\underline{E}(\underline{\xi},t)$ satisfies the reaction-diffusion equation

$$\frac{\partial \underline{E}(\underline{\xi},t)}{\partial t} = \underline{f}(\underline{\xi},t,\underline{E}) + \nabla \cdot [\mathbf{D}(\underline{\xi})\nabla \underline{E}(\underline{\xi},t)] \tag{5.1}$$

under these assumptions, where $\nabla := (\frac{\partial}{\partial x}, \frac{\partial}{\partial y})$, and where $\underline{f}(\underline{\xi},t,\underline{E}) = [f_1(\underline{\xi},t,\underline{E}), \ldots, f_{11}(\underline{\xi},t,\underline{E})]^T$ contains as its i-th entry the number of the i-th population created during time t. More specifically,

$$\begin{aligned}
f_1(\underline{\xi},t,\underline{E}) &= 0.5(\gamma(\underline{\xi},t)\lambda_f + \beta\rho(\underline{\xi},t)\lambda_s)E_9(\underline{\xi},t) - (\mu_E(t,\tau) + \alpha_E(t,\tau))E_1(\underline{\xi},t),\\
f_2(\underline{\xi},t,\underline{E}) &= 0.5(1-\beta)\rho(\underline{\xi},t)\lambda_s E_9(\underline{\xi},t) - (\mu_E(t,\tau) + \alpha_E(t,\tau))E_2(\underline{\xi},t),\\
f_3(\underline{\xi},t,\underline{E}) &= \alpha_E(t,\tau)E_1(\underline{\xi},t) - (\mu_{L_1}(\underline{\xi},t,\tau) + \alpha_{L_1}(t,\tau))E_3(\underline{\xi},t),\\
f_4(\underline{\xi},t,\underline{E}) &= \alpha_E(t,\tau)E_2(\underline{\xi},t) - (\mu_{L_1}(\underline{\xi},t,\tau) + \alpha_{L_1}(t,\tau))E_4(\underline{\xi},t),\\
f_5(\underline{\xi},t,\underline{E}) &= \alpha_{L_1}(t,\tau)E_3(\underline{\xi},t) - (\mu_{L_2}(\underline{\xi},t,\tau)\left(1 + b(\underline{\xi},t)((E_5+E_6)(\underline{\xi},t))\right) + \alpha_{L_2}(t,\tau))E_5(\underline{\xi},t),\\
f_6(\underline{\xi},t,\underline{E}) &= \alpha_{L_1}(t,\tau)E_4(\underline{\xi},t) - (\mu_{L_2}(\underline{\xi},t,\tau)\left(1 + b(\underline{\xi},t)((E_5+E_6)(\underline{\xi},t))\right) + \alpha_{L_2}(t,\tau))E_6(\underline{\xi},t),\\
f_7(\underline{\xi},t,\underline{E}) &= \alpha_{L_2}(t,\tau)E_5(\underline{\xi},t) - (\mu_P(t,\tau) + \alpha_P(t,\tau))E_7(\underline{\xi},t),\\
f_8(\underline{\xi},t,\underline{E}) &= \alpha_{L_2}(t,\tau)E_6(\underline{\xi},t) - (\mu_P(t,\tau) + \alpha_P(t,\tau))E_8(\underline{\xi},t),\\
f_9(\underline{\xi},t,\underline{E}) &= \alpha_P(t,\tau)E_7(\underline{\xi},t) - \mu_M(t,\tau)E_9(\underline{\xi},t),
\end{aligned}$$

$$f_{10}(\underline{\xi},t,\underline{E}) = \alpha_P(t,\tau)E_8(\underline{\xi},t) - \mu_M(t,\tau)E_{10}(\underline{\xi},t),$$

$$f_{11}(\underline{\xi},t,\underline{E}) = r(\underline{\xi},t) - \mu_S(t,\tau)E_{11}(\underline{\xi},t),$$

Note that $\underline{f}(\underline{\xi},t,\underline{E})$ is the spatial equivalent of (4.2), where λ_f and λ_s denote the egg laying rates of a fertile female mated with a fertile and released male, respectively, $\gamma(\underline{\xi},t)$ and $\rho(\underline{\xi},t)$ denote the probabilities of a fertile egg being fertilized by a fertile or semi-sterile sperm at position $\underline{\xi}$ and time t, respectively, $\mu_E(t,\tau)$, $\mu_P(t,\tau)$ and $\mu_M(t,\tau)$ denote the stage-specific mortality rates at time t at a temperature of τ degrees and $\mu_L(\underline{\xi},t,\tau)$ denotes the larval mortality rate at position $\underline{\xi}$, at time t and at a temperature of τ degrees. Furthermore, $b(\underline{\xi},t)$ denotes the density-dependent mortality parameter at position $\underline{\xi}$ and time t, and $\alpha_E(t,\tau)$, $\alpha_L(t,\tau)$ and $\alpha_P(t,\tau)$ denote the egg, larval and pupal maturation rates at time t and at a temperature of τ degrees, respectively, while $r(\underline{\xi},t)$ denotes the sterile release rate at position $\underline{\xi}$ and time t. Finally, β denotes the fraction of eggs from the F_1 progeny of released sterile males which is fertile [85].

In order to be able to compare solutions of a variety of different scenarios in terms of initial conditions over the spatial domain, equation (5.1) has to be expressed in terms of non-dimensional variables. If we let

$$x_1 = \frac{\xi_1}{\mathcal{L}},\ x_2 = \frac{\xi_2}{\mathcal{L}},\ \mathbf{D}(\underline{x}) = \mathbf{D}(\underline{\xi}),\ E_n(\underline{x},t) = \frac{E_n(\underline{\xi},t)}{\mathcal{L}^2},\ \mathcal{E}_i(\underline{x},t) = E_i(\underline{x},t) \text{ and } \mathcal{E}_j(\underline{x},t) = \frac{E_j(\underline{x},t)}{E_j(\underline{x},0)}$$

for $n = 1,\ldots,9$, $i = 2,4,6,8,10,11$ and for $j = 1,3,5,7,9$, where $\mathcal{L}$ denotes the length in metres of the domain and $E_i(\underline{\xi},0)$ denotes the initial fertile population densities at position $\underline{\xi}$ and at time $t = 0$, then

$$\frac{\partial \underline{E}}{\partial \xi_1} = \frac{\partial \underline{E}}{\partial x_1}\frac{\partial x_1}{\partial \xi_1} = \frac{\partial \underline{E}}{\partial x_1}\frac{1}{\mathcal{L}}, \tag{5.2}$$

$$\frac{\partial \underline{E}}{\partial \xi_2} = \frac{\partial \underline{E}}{\partial x_2}\frac{\partial x_2}{\partial \xi_2} = \frac{\partial \underline{E}}{\partial x_2}\frac{1}{\mathcal{L}}, \tag{5.3}$$

$$\frac{\partial^2 \underline{E}}{\partial \xi_1^2} = \frac{\partial}{\partial x_1}\left(\frac{1}{\mathcal{L}}\frac{\partial \underline{E}}{\partial x_1}\right)\frac{\partial x_1}{\partial \xi_1} = \frac{\partial^2 \underline{E}}{\partial x_1^2}\frac{1}{\mathcal{L}^2} \text{ and} \tag{5.4}$$

$$\frac{\partial^2 \underline{E}}{\partial \xi_2^2} = \frac{\partial}{\partial x_2}\left(\frac{1}{\mathcal{L}}\frac{\partial \underline{E}}{\partial x_2}\right)\frac{\partial x_2}{\partial \xi_2} = \frac{\partial^2 \underline{E}}{\partial x_2^2}\frac{1}{\mathcal{L}^2}. \tag{5.5}$$

Substituting (5.2) to (5.5) into (5.1) and simplifying yields

$$\frac{\partial \underline{\mathcal{E}}(\underline{x},t)}{\partial t} = \underline{f}\left(\underline{x},t,\underline{\mathcal{E}}(\underline{x},t)\frac{E_j(\underline{x},0)}{E_i(\underline{x},0)}\right) + \frac{1}{\mathcal{L}^2}\nabla\cdot[\mathbf{D}(\underline{x})\nabla\underline{\mathcal{E}}(\underline{x},t)]. \tag{5.6}$$

where $0 < x_1 \leq a$, $0 < x_2 \leq b$ and $j = 1,3,5,7,9$. If the non-dimensional spatial domain is divided into a 2-dimensional $a \times b$ rectangular grid topology with grid points of intersection at $x_1^r = rh$ and $x_2^s = sh$, where $r = 0,\cdots,m$, $s = 0,\cdots,n$, $mh = a$ and $nh = b$, then the one finite-difference approximation to (5.6) is

$$\frac{\underline{\mathcal{E}}(\underline{x},t+k) - \underline{\mathcal{E}}(\underline{x},t)}{k} = \underline{f}\left(\underline{x},t,\underline{\mathcal{E}}(\underline{x},t)\frac{E_j(\underline{x},0)}{E_i(\underline{x},0)}\right) + \frac{1}{\mathcal{L}^2}\left(\nabla\mathbf{D}(\underline{x})\cdot\nabla\underline{\mathcal{E}}(\underline{x},t) + \mathbf{D}(\underline{x})\nabla^2\underline{\mathcal{E}}(\underline{x},t)\right).$$

In the equation above,

$$\nabla G(\underline{x},t) = \left(\frac{1}{2h}\left(G(x_1+h,x_2,t)-G(x_1-h,x_2,t)\right), \frac{1}{2h}\left(G(x_1,x_2+h,t)-G(x_1,x_2-h,t)\right)\right)$$

is the central-difference approximation and

$$\begin{aligned}\nabla^2 G(\underline{x},t) &= \frac{1}{h^2}\left(G(x_1+h,x_2,t)+G(x_1-h,x_2,t)+G(x_1,x_2+h,t)+G(x_1,x_2-h,t)\right.\\ &\quad \left.-4G(x_1,x_2,t)\right)\end{aligned}$$

is known as the discretised Laplacian operator for diffusion, with both spatial approximations having a leading error of order h^2 [96]. The rectangular grid topology corresponds to a set of adjacent sugarcane fields divided into discrete patches of sugarcane, each patch (node) having the same number of sugarcane stalks and being small enough so that the mean-field approximation may be adopted within a single patch. This patchy environment is modelled as a two-dimensional arena in which *E. saccharina* populations are distributed amongst the grid points (nodes) with populations in neighbouring nodes connected by dispersing individuals. The proportion of moths dispersing is calculated by using the differences of the combined fertile and sterile moth population densities between the four neighbouring nodes of any given node. Under the assumption that dispersal only occurs during the night, a discrete time model for diffusion is appropriate. If t is measured in days and $k = 1$, a discrete time model for population growth (similar to the mean-field model described in §4.3) and diffusion is obtained, with diffusion being continuous in space. Since no approximation is required in terms of time, the discretized model therefore only has approximating errors with respect to space, which gives a leading error of order h^2. As h tends to zero, the finite-difference approximation tends to the true solution [96].

5.3.1 Boundary conditions

Since *E. saccharina* moths seem to exhibit a hierarchical choice with respect to host plant habitat for ovipositing, it is possible that in a spatial domain surrounded by more favourable habitats, a certain proportion of migrants will leave the domain and populate the surrounding areas. The flux at the boundary is assumed constant, therefore Neumann boundary conditions are assumed with

$$\left.\frac{\partial \underline{\mathcal{E}}(x_1,x_2,t)}{\partial x_1}\right|_{\partial\mathcal{S}} = \eta, \tag{5.7}$$

$$\left.\frac{\partial \underline{\mathcal{E}}(x_1,x_2,t)}{\partial x_2}\right|_{\partial\mathcal{S}} = \eta, \tag{5.8}$$

where $\partial\mathcal{S}$ is the boundary of $\mathcal{S}$. Assuming the boundary is not part of $\mathcal{S}$, and letting the boundary nodes be situated at positions $x_1 = x_1^{-1}$ and $x_1 = x_1^{m+1}$ for all x_2, and $x_2 = x_2^{-1}$ and $x_2 = x_2^{n+1}$ for all x_1, the value of $\underline{\mathcal{E}}$ for $x_1^{-1} < x_1 < x_1^{m+1}$ and $x_2^{-1} < x_2 < x_2^{n+1}$ is known since it is in the model domain. The Taylor expansion of $\underline{\mathcal{E}}$ around x_1^{-1} up to second order is given by

$$\underline{\mathcal{E}}(x_1^{-1}+h,x_2,t) = \underline{\mathcal{E}}(x_1^{-1},x_2,t) + h\frac{\partial}{\partial x_1}\underline{\mathcal{E}}(x_1^{-1},x_2,t) + \frac{h^2}{2}\frac{\partial}{\partial x_1^2}\underline{\mathcal{E}}(x_1^{-1},x_2,t) + \mathcal{O}(h^3),$$

$$\underline{\mathcal{E}}(x_1^{-1}+2h,x_2,t) = \underline{\mathcal{E}}(x_1^{-1},x_2,t) + 2h\frac{\partial}{\partial x_1}\underline{\mathcal{E}}(x_1^{-1},x_2,t) + 2h^2\frac{\partial}{\partial x_1^2}\underline{\mathcal{E}}(x_1^{-1},x_2,t) + \mathcal{O}(h^3).$$

Similar expansions of $\underline{\mathcal{E}}$ around x_1^{m+1}, x_2^{-1} and x_2^{n+1} may be obtained. By imposing the boundary conditions (5.7) and (5.8), and substituting the known values for $\underline{\mathcal{E}}(x_1^0, x_2, t)$, $\underline{\mathcal{E}}(x_1^1, x_2, t)$, $\underline{\mathcal{E}}(x_1, x_2^0, t)$, $\underline{\mathcal{E}}(x_1, x_2^1, t)$, $\underline{\mathcal{E}}(x_1^m, x_2, t)$, $\underline{\mathcal{E}}(x_1^{m-1}, x_2, t)$, $\underline{\mathcal{E}}(x_1, x_2^n, t)$ and $\underline{\mathcal{E}}(x_1, x_2^{n-1}, t)$ yields the boundary values

$$\begin{aligned}
\underline{\mathcal{E}}(x_1^{-1}, x_2, t) &= \frac{4\underline{\mathcal{E}}(x_1^0, x_2, t) - \underline{\mathcal{E}}(x_1^1, x_2, t) - 2h\eta}{3},\\
\underline{\mathcal{E}}(x_1, x_2^{-1}, t) &= \frac{4\underline{\mathcal{E}}(x_1, x_2^0, t) - \underline{\mathcal{E}}(x_1, x_2^1, t) - 2h\eta}{3},\\
\underline{\mathcal{E}}(x_1^{m+1}, x_2, t) &= \frac{4\underline{\mathcal{E}}(x_1^m, x_2, t) - \underline{\mathcal{E}}(x_1^{m-1}, x_2, t) - 2h\eta}{3},\\
\underline{\mathcal{E}}(x_1, x_2^{n+1}, t) &= \frac{4\underline{\mathcal{E}}(x_1, x_2^n, t) - \underline{\mathcal{E}}(x_1, x_2^{n-1}, t) - 2h\eta}{3}.
\end{aligned}$$

In this dissertation, however, it is assumed that the spatial domain is isolated and surrounded by land uses not corresponding to possible habitats for *E. saccharina* Walker. Zero-flux Neumann boundary conditions are therefore assumed ($\eta = 0$) which results in migrants on the edge nodes of the domain being prevented from crossing the boundary $\partial\mathcal{S}$. If migrants are prevented from leaving the domain, then $\sum_{\underline{x}} \nabla\mathbf{D}(\underline{x}) \cdot \nabla\underline{\mathcal{E}}(\underline{x}, t) + \mathbf{D}(\underline{x})\nabla^2\underline{\mathcal{E}}(\underline{x}, t) = 0$. In order to calculate $\nabla\mathbf{D}$, boundary conditions for $\mathbf{D}$ must also be specified. The Taylor expansion of $\mathbf{D}$ around x_1^{-1} is given by

$$\mathbf{D}(x_1^{-1} + h, x_2) = \mathbf{D}(x_1^{-1}, x_2) + h\frac{\partial}{\partial x_1}\mathbf{D}(x_1^{-1}, x_2) + \frac{h^2}{2}\frac{\partial}{\partial x_1^2}\mathbf{D}(x_1^{-1}, x_2) + \mathcal{O}(h^3), \tag{5.9}$$

$$\mathbf{D}(x_1^{-1} + 2h, x_2) = \mathbf{D}(x_1^{-1}, x_2) + 2h\frac{\partial}{\partial x_1}\mathbf{D}(x_1^{-1}, x_2) + 2h^2\frac{\partial}{\partial x_1^2}\mathbf{D}(x_1^{-1}, x_2) + \mathcal{O}(h^3). \tag{5.10}$$

Similar expansions of $\mathbf{D}$ around x_1^{m+1}, x_2^{-1} and x_2^{n+1} may be obtained. None of the values or derivatives are known on the boundary. From (5.10) and ignoring the higher order terms,

$$h\frac{\partial}{\partial x_1}\mathbf{D}(x_1^{-1}, x_2) + h^2\frac{\partial}{\partial x_1^2}\mathbf{D}(x_1^{-1}, x_2) = \frac{1}{2}\mathbf{D}(x_1^{-1} + 2h, x_2) - \frac{1}{2}\mathbf{D}(x_1^{-1}, x_2),$$

and therefore

$$h\frac{\partial}{\partial x_1}\mathbf{D}(x_1^{-1}, x_2) + \frac{h^2}{2}\frac{\partial}{\partial x_1^2}\mathbf{D}(x_1^{-1}, x_2) = \frac{1}{2}(1-k)\mathbf{D}(x_1^{-1} + 2h, x_2) - \frac{1}{2}k\mathbf{D}(x_1^{-1}, x_2) \tag{5.11}$$

for some constant k. Substituting (5.11) into (5.9) (for all similar boundary expansions) and simplifying, yields the boundary values

$$\begin{aligned}
\mathbf{D}(x_1^{-1}, x_2) &= \frac{2}{2-k}\mathbf{D}(x_1^0, x_2) - \frac{1-k}{2-k}\mathbf{D}(x_1^1, x_2),\\
\mathbf{D}(x_1, x_2^{-1}) &= \frac{2}{2-k}\mathbf{D}(x_1, x_2^0) - \frac{1-k}{2-k}\mathbf{D}(x_1, x_2^1),\\
\mathbf{D}(x_1^{-1}, x_2) &= \frac{2}{2-k}\mathbf{D}(x_1^m, x_2) - \frac{1-k}{2-k}\mathbf{D}(x_1^{m-1}, x_2),\\
\mathbf{D}(x_1^{-1}, x_2) &= \frac{2}{2-k}\mathbf{D}(x_1, x_1^n) - \frac{1-k}{2-k}\mathbf{D}(x_1, x_2^{n-1}).
\end{aligned}$$

The constant k is chosen such that $\sum_{\underline{x}} \nabla \mathbf{D}(\underline{x}) \cdot \nabla \underline{\mathcal{E}}(\underline{x}, t) + \mathbf{D}(\underline{x}) \nabla^2 \underline{\mathcal{E}}(\underline{x}, t) = 0$. For a homogenous domain, $k = -1$, and all boundary values for $\mathbf{D}(\underline{x})$ are equal to 0[1].

5.3.2 Initial values

Initial values of fertile egg, larval, pupal and moth population densities are again computed according to the relations

$$\frac{\lambda_f}{\mu_E + \alpha_E} : \frac{\lambda_f \alpha_E}{(\mu_E + \alpha_E)(\mu_{L_1} + \alpha_{L_1})} : \frac{\mu_M(\mu_P + \alpha_P)}{\alpha_{L_2} \alpha_P} : \frac{\mu_M}{\alpha_P} : 1$$

between the equilibrium population densities of the *E. saccharina* mean-field model with no sterile releases. Mortality and maturation rates at temperature τ and at time $t = 0$ are used in the initial value calculation. The initial populations are assumed to be uniformly distributed within a field in $\mathcal{S}$. In a newly planted sugarcane field, an initial *E. saccharina* population density of e/100s ≤ 1 is assumed, where e/100s denotes the number of larvae found per 100 stalks. In a more mature sugarcane field, depending on the sugarcane variety and the age of the sugarcane, an initial *E. saccharina* population density of e/100s > 1 is assumed.

5.4 Model input parameters

The population growth input parameters of the model described in §5.3 have all been described in §4.4. In the spatio-temporal model mortality parameters vary across $\mathcal{S}$ according to cane age and variety. Diffusion coefficients are assumed constant across $\mathcal{S}$, whereas the release rate varies across $\mathcal{S}$ according to the release method. Possible values for the diffusion coefficients have been obtained from simulations.

5.4.1 Diffusion coefficients

In general, the diffusion coefficient is defined as the rate of transfer of the diffusing substance across a unit area of a section, divided by the space gradient of concentration at the section [37]. The SI unit for the diffusion coefficient is m^2/s [72]. In this study the diffusion coefficient is defined as the number of moths that diffuse (disperse) across a unit area of 25 m^2 per day at a certain position in the cane field under the influence of a spatial gradient of one moth. The diffusion coefficient $d(\underline{x})$ is a measure of how effectively moths disperse between neighbouring nodes at position $\underline{x} = [x_1, x_2]^T$. The use of a pure diffusion process with constant diffusion coefficients in this study (in terms of both space and time) is based on the assumption that individual moths follow a pure random walk. As mentioned in §5.2, this assumption is only realistic if individual moths have no long-term memory or large-scale knowledge of the landscape [79]. At the time of this study, not much was known about the dispersal patterns of individual *E. saccharina* moths. A study by Berry *et al.* [16] revealed that *E. saccharina* was able to colonize most of a 0.65 ha field during the crop cycle with invasions both from nearby fields and internal spread within the field. No measure of the rate of dispersal for *E. saccharina* moths

[1] The more common way to deal with a homogenous domain where diffusion coefficients are constant is to apply $\sum \nabla \cdot [\mathbf{D} \nabla \underline{\mathcal{E}}(\underline{x}, t)] = \sum \mathbf{D} \nabla^2 \underline{\mathcal{E}}(\underline{x}, t) = 0$, with the boundary values for $\underline{\mathcal{E}}(\underline{x}, t)$ equal to the value of the nearest node inside the domain. Both methods yield the same solution for $\nabla \cdot [\mathbf{D}(\underline{x}) \nabla \underline{\mathcal{E}}(\underline{x}, t)]$ at position $\underline{x}$. However, for variable diffusion coefficients, only the boundary method described in this chapter yields a solution such that $\sum_{\underline{x}} \nabla \mathbf{D}(\underline{x}) \cdot \nabla \underline{\mathcal{E}}(\underline{x}, t) + \mathbf{D}(\underline{x}) \nabla^2 \underline{\mathcal{E}}(\underline{x}, t) = 0$.

was available. If the diffusion coefficient is assumed less than or equal to the average gradient between the four neighbouring nodes in the finite-difference approximation, then $|d(\underline{x})| \leq \frac{1}{4}$ for $h = \frac{1}{\mathcal{L}}$. A possible range of $0.005 < |d(\underline{x})| < 0.03$ was obtained from simulations performed on a 1 ha field with initial infestation occurring only at one node in the middle of the field. For diffusion coefficients outside this range, infestation seemed either too concentrated around the initial patch, or too widespread to correspond to the observation by Berry *et al.* [16] (see Figure 5.1).

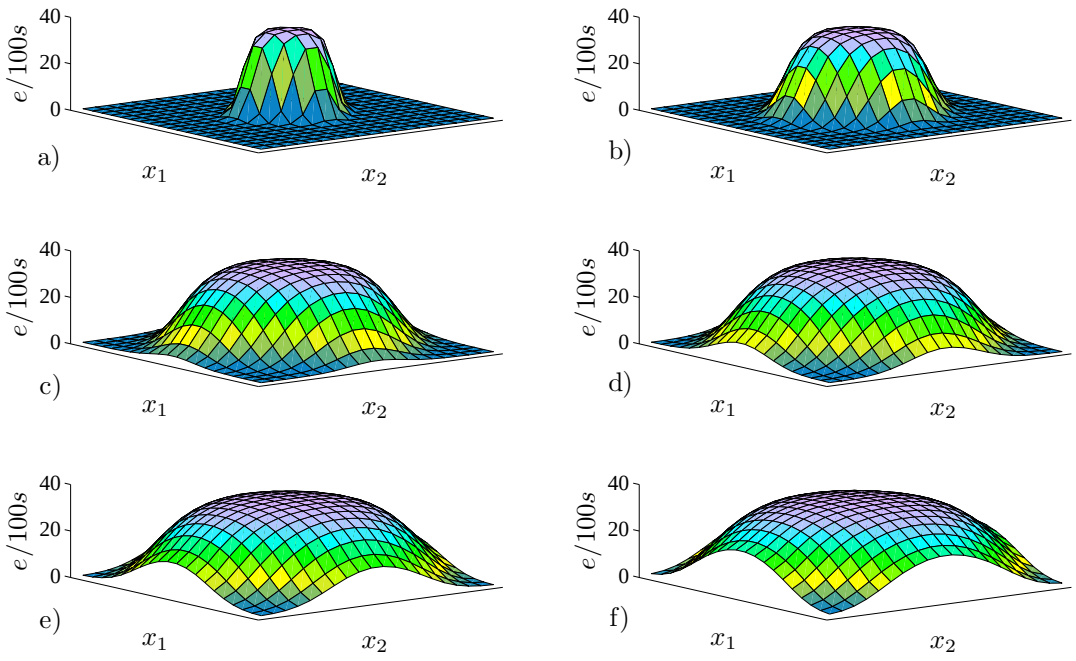


FIGURE 5.1: *Moth population densities at the end of the crop cycle for different diffusion coefficients where (a)* $d(x_1, x_2) = 0.001$, *(b)* $d(x_1, x_2) = 0.005$, *(c)* $d(x_1, x_2) = 0.015$, *(d)* $d(x_1, x_2) = 0.02$, *(e)* $d(x_1, x_2) = 0.025$, *(f)* $d(x_1, x_2) = 0.03$.

5.4.2 Release rate

Two methods of releasing sterile moths are assumed in the spatio-temporal model. These methods are releasing sterile moths from an ATV driven alongside the edge of each sugarcane field (in release lanes) and releasing moths from an aircraft.

SIT releases by means of ATVs being driven alongside the edge of a sugarcane field may result in a uniform distribution of sterile moths along the release lanes if mechanical release devices are used to release moths. However, if releases are performed manually, a discrete distribution of sterile moths along the release lanes at specific release points is applicable. Figure 5.2 illustrates the two types of release distributions for ATV releases. The release rate $r(\underline{x}, t)$ at position $\underline{x} = [x_1, x_2]^T$ is therefore obtained by distributing the required number of released sterile moths uniformly across all patches within the release lanes (or at discrete points), with $r(\underline{x}, t) = 0$ in all other patches. The release lanes of the different sugarcane fields are defined according to the assumed field layout within the spatial domain.

Releasing sterile moths from an aircraft has been demonstrated to result in a uniform distribution of sterile moths across the entire release area if the aircraft has the capability of flying along

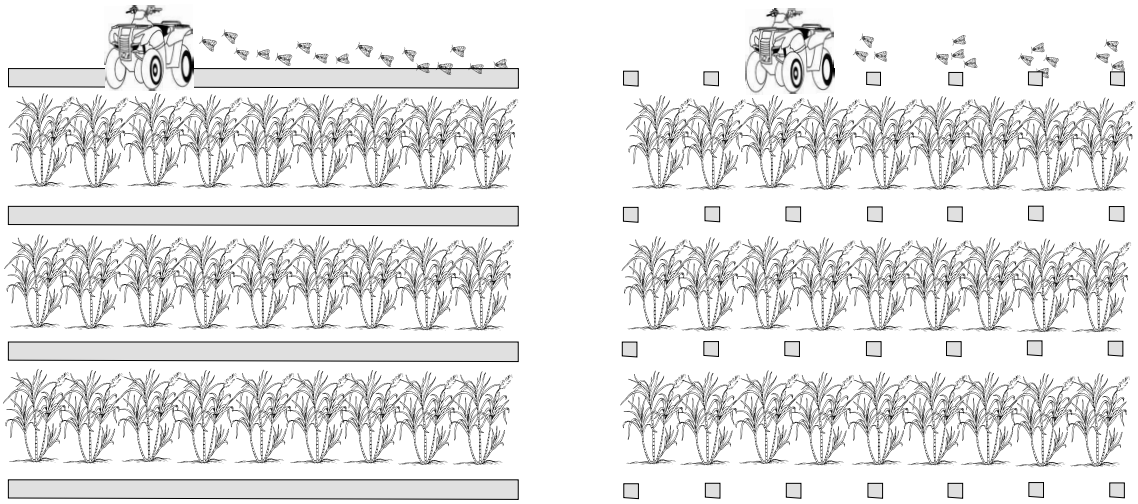


FIGURE 5.2: *(a) Mechanical release devices release moths at a constant rate from an ATV, resulting in a uniform distribution along the release lane. (b) If moths are released by hand, releases occur at specific release points.*

predetermined equally spaced release paths [101]. Achieving a uniform distribution, however, depends significantly on the dispersal capability of the insect and the corresponding choice of release paths. The number of moths released along the flight paths may be assumed to spread according to a gaussian distribution before reaching the canopy (fewer moths disperse further from the original release lane before reaching the canopy). The more the distributions along the flight paths overlap, the closer to a uniform distribution across the entire domain (see Figure 5.3). If an approximate uniform distribution is obtained, the model of Chapter 4 may be assumed. Release flight paths in SIT programmes usually range between 100 and 500 metres apart and depends on the species' capability to disperse [40]. A closer spacing is required for weak fliers [40], as may be the case for *E. saccharina*. In this chapter, sterile moths are assumed to be released along equally spaced predetermined release paths 100 metres apart, but not necessarily resulting in a uniform distribution of sterile moths across the entire spatial domain (distributions do not overlap). The position of the release paths is, however, assumed either constant over time, or variable over time. The smallest width of the release distribution and release ratio at which suppression may still be obtained may then be determined assuming release paths are either always at the same positions, or varying in positions. Released moths are assumed to spread up to a 100 m (50 m in both directions) before reaching the canopy, therefore no overlapping of distributions are assumed on the release day (one time step). If the positions of the release paths are, however, variable over time, overlapping of distributions may occur over time. The release rate $r(\underline{x}, t)$ at position $\underline{x} = [x_1, x_2]^T$ is obtained by distributing the total number of released sterile moths according to a gaussian distribution in the area under the equally spaced flight paths of 100 metres apart (see Figure 5.3). No sterile releases are assumed in the areas between the distributions.

5.4.3 Variability in $\mathcal{S}$

Homogenous patches are assumed within each subset (a single field) of $\mathcal{S}$. As a result of the uniform environment, mortality and diffusion parameters are assumed to be spatially homogenous within a subset. The different subsets of the spatial domain $\mathcal{S}$ are assumed heterogeneous with

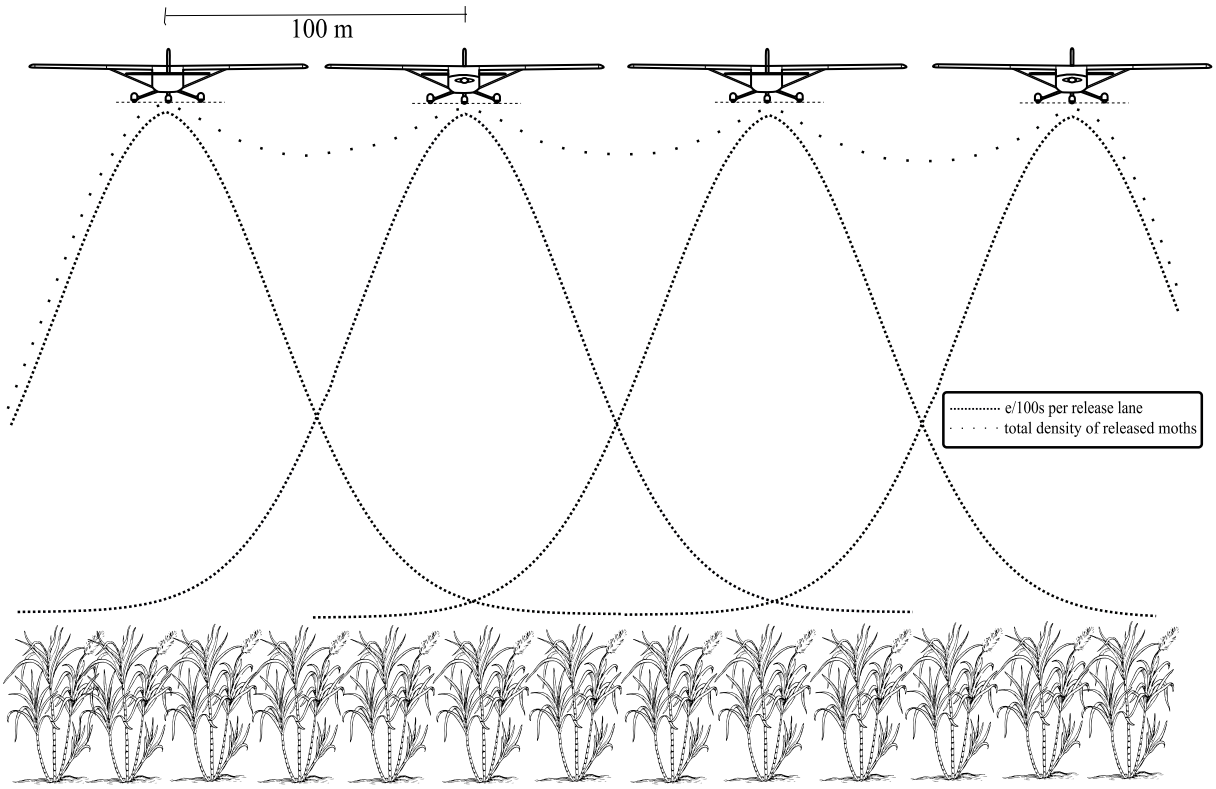


FIGURE 5.3: *Moths released from an aircraft are assumed to spread according to a gaussian distribution before reaching the canopy.*

respect to sugarcane variety and age, which in turn results in mortality parameters being spatially heterogeneous across $\mathcal{S}$. As a result of crop varieties having different resistance levels with respect to *E. saccharina* infestation, the larval mortality parameter in each subset of $\mathcal{S}$ varies according to the crop variety in the field (see the discussion in §4.4.3). Also, for differently aged crops, the larval mortality in each subset of $\mathcal{S}$ is increased by a density-dependent mortality parameter according to the age of the crop within the specific subset. The density-dependent parameter decreases with age, resulting in a higher carrying capacity for older crops as a result of higher nutrition levels for *E. saccharina* (see the discussion in §4.4.4).

If *E. saccharina* moths prefer certain cane varieties or cane ages, the value associated with the diffusion coefficient may vary across $\mathcal{S}$ according to the variety and age of the cane at the specific position. Diffusion coefficients may therefore be heterogeneous across $\mathcal{S}$. However, in this chapter, dispersal is assumed to occur randomly in any direction without any directive movement. Homogenous diffusion coefficients are therefore assumed across $\mathcal{S}$.

Heterogeneous patches may also result in a heterogeneous release rate $r(\underline{x}, t)$ across the spatial domain. For a given release ratio, the release rate may need to be higher for older cane patches as a result of higher infestation levels at time $t = 0$. Furthermore, given the release methods and assumed distributions of released sterile moths, $r(\underline{x}, t)$ is not homogenous across $\mathcal{S}$.

5.5 Model output parameters

For the purposes of the spatio-temporal model in §5.3, a sterile release strategy is defined as the minimum number, given a certain initial infestation level, release method and frequency of

releases, of sterile insects to release in order to suppress a native *E. saccharina* population. In order to evaluate the effect of different sterile release strategies on an *E. saccharina* infested area, a crop damage index similar to the index defined in §4.5.3 may serve as an indicator of the damage caused by *E. saccharina*. The crop damage index is again used to estimate the losses in revenue due to *E. saccharina* infestation and the estimated cost of the release strategy is compared to the estimated increase in revenue in order to evaluate the economic viability of a release strategy.

5.5.1 The cost of a release strategy

In order to estimate the cost of a release strategy, three costs are taken into account in this study, namely the cost κ_r of raising and sterilising one *E. saccharina* moth, the labour cost κ_ℓ involved per day per hectare for releasing sterile moths, and the fuel cost κ_f per ha involved in transporting the sterilised moths on the release site. Transportion cost to a release site is not included in the cost estimation. The value of κ_r is again assumed to range between R0.03 and R0.10.

The SIT rearing facilities in South Africa perform sterile releases with ATVs. Entomon Technologies (Pty) Ltd uses two ATVs for performing releases in infested areas and one Kia K2700 for transportation to the release site. Data indicate that the labour cost κ_ℓ is approximately R5.00 per hectare [99, 120], but differs from company to company. The fuel cost κ_f based on the current diesel price of R9.20 per litre and assuming an average fuel consumption of 40 km per litre for an ATV, is approximately R0.023 for every 100 m driven. If, for example, ATVs drive in release lanes 30 m apart on a 100×100 m area, $\kappa_f = 0.09$. The labour and fuel costs for aerial releases are as mentioned in §4.5.2, namely ranging between R4.76 and R23.80 per hectare.

The total cost of a release strategy is given by

$$C = \sum_{j=0}^{t} \kappa_r \left(\sum_{\underline{x}} r(\underline{x}, j) \right) + \phi(j) h (\kappa_\ell + \kappa_f), \tag{5.12}$$

where $r(\underline{x}, j) = 1\,300 \eta h_p e_9$ denotes the release rate at position $\underline{x}$ on day j and $\phi(j)$ denotes a Bernoulli variable which takes the value 1 if sterile moths are released on day j, or 0 otherwise. Furthermore, h_p denotes the area (in hectares) of a patch and h denotes the area in hectares of the spatial domain[2].

5.5.2 Crop damage index

A damage index (similar to the damage index described in §4.5.3), $\delta(\underline{x}, t)$, on any day t at position $\underline{x}$ is defined as the cumulative total of larvae feeding up to day t at position $\underline{x}$ since the crop was planted, measured as a percentage of the total of stalk length on day t, and is given by

$$\delta(\underline{x}, t) = \frac{\sum_{j=0}^{t} \sigma(j) (\mathcal{E}_5(\underline{x}, j) + \mathcal{E}_6(\underline{x}, j))}{\ell(\underline{x}, t)}, \tag{5.13}$$

where $\sigma(j)$ denotes the amount of larval feeding per larvae on day j and where $\ell(\underline{x}, t)$ denotes the average stalk length on day t at position $\underline{x}$. In (5.13), σ is an estimation of the length

[2] A one hectare field contains, on average, 130 000 stalks in South Africa. An infestation of 1 $e/100s$ is therefore equivalent to 1 300 larvae per hectare, as mentioned before.

of stalk bored per larvae per degree-day in terms of chronological days. The estimated values of σ for different temperatures are given in Table 4.5. Furthermore, $\ell(\underline{x}, t)$ is an estimation (measured in mm) of the average stalk length on day t at position $\underline{x}$, given by

$$\ell(\underline{x}, t+1) = \ell(\underline{x}, t) + 0.16(24)(-1.32 + 0.176(\tau - 10)) \tag{5.14}$$

for a two-year cycle crop, where $\ell(\underline{x}, 0)$ denotes the average stalk length at position $\underline{x} = [x_1, x_2]^T$ at time $t = 0$.

5.5.3 Increase in revenue

The percentage sucrose, $S(\underline{x})$, of mature sugarcane at position $\underline{x}$ and at harvest time t is given by

$$S(\underline{x}) = 100\frac{-1.31\delta(\underline{x}, t) + 84}{-5.78\delta(\underline{x}, t) + 556}, \tag{5.15}$$

where the numerator denotes the sucrose mass measured in g/stalk, while the denominator denotes the stalk mass (also measured in g/stalk), and where $\delta(\underline{x}, t)$ denotes the percentage internodes bored in mature sugarcane at position $\underline{x}$, obtained from (5.13). The RV percentage at position $\underline{x}$ is obtained from (4.43). In order to calculate the payment due to a farmer, the revenue W is given by

$$W = 2817.05 \sum_{\underline{x}} T(\underline{x}) \frac{RV(\underline{x})}{100}, \tag{5.16}$$

where $T(\underline{x})$ denotes the average number of tons of sugarcane delivered at position $\underline{x} = [x_1, x_2]^T$, namely $0.13h_p(-5.78\delta(\underline{x}, t) + 556)$, where h_p denotes the size of the habitat patch at position $\underline{x}$ (measured in hectares). The increase in revenue as a result of SIT is given by (4.46) and the profit made as a result of SIT is given by (4.47).

5.6 Model verification

As mentioned in §4.6, it is necessary to verify whether the implementation of the model described in §5.3 represents a correct representation of the logic contained in the mathematical description of the model. The model was implemented in Mathworks' MATLAB (R2009a) and all simulations reported here were performed for a field size of 1 ha (100 m × 100 m), each patch having a size of 25m^2. For the purposes of verification, the following domains are defined.

Definition 5.1 *Let $\mathcal{S}_p$ denote the domain having a node at position $\underline{x} = [x_1^{\frac{m}{2}}, x_2^{\frac{n}{2}}]^T$ and let $\mathcal{S}_{p'}$ denote the domain having nodes at positions $\underline{x} = [x_1^i, x_2^j]^T$ with $i \neq \frac{m}{2}$ and $j \neq \frac{n}{2}$.*

Definition 5.2 *Let $\mathcal{S}_s$ denote the domain having nodes at positions $\underline{x} = [x_1^{i'}, x_2^j]^T$, with $i' \in \{1, \ldots, \frac{m}{2}\}$ and $j \in \{1, \ldots, n\}$ and let $\mathcal{S}_{s'}$ denote the domain having nodes at positions $\underline{x} = [x_1^{i''}, x_2^j]^T$ with $i'' \in \{\frac{m}{2} + 1, \ldots, m\}$ and $j \in \{1, \ldots, n\}$.*

5.6.1 Homogenous domain

Assuming that all nodes are homogenous with respect to initial infestation level, sterile release rate, cane variety and cane age, the spatio-temporal model is expected to yield the same results

as the mean-field model described in Chapter 4. In order to test whether the spatio-temporal model implementation responds likewise, simulations were performed with and without sterile releases over a time period of 24 months. For simulations performed with and without sterile releases, infestation levels increase to the same level as those in the mean-field model (see Figures 5.4 and 5.5). The model implementation, therefore, responds as expected when compared to the mean-field model.

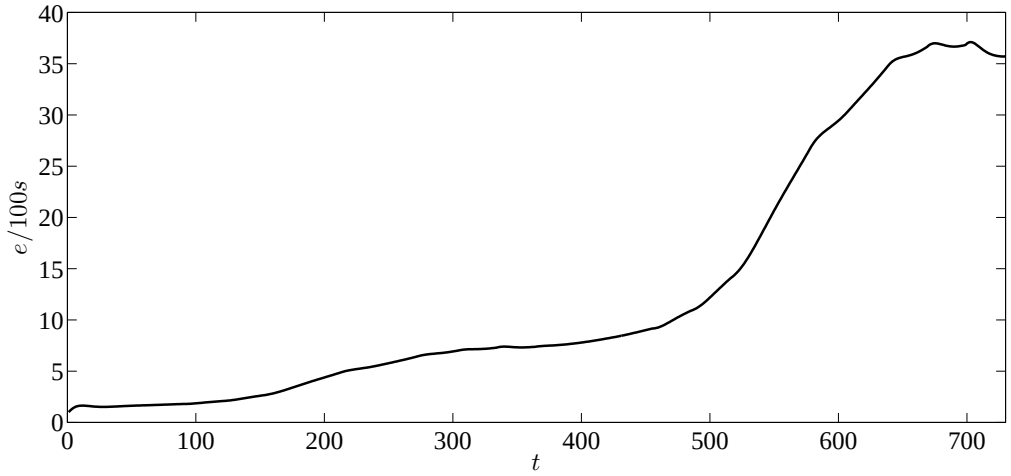


FIGURE 5.4: *Simulations of larval population densities from the mean-field model yield the same results as simulations of average larval population densities from the spatial model when no sterile moths are released. The two models yield the same result only if the nodes across the entire domain are homogenous with respect to initial infestation level, cane variety and cane age.*

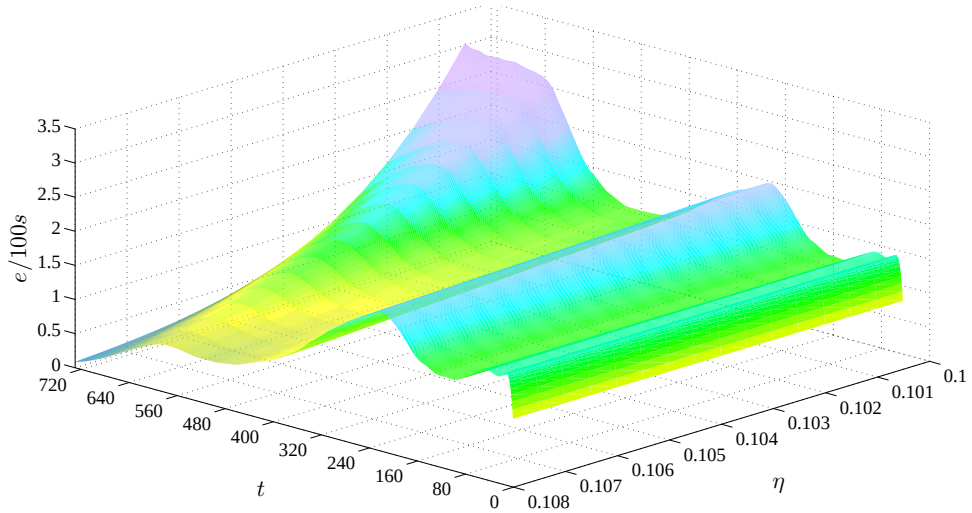


FIGURE 5.5: *Simulations of larval population densities from the mean-field model yield the same results as simulations of average larval population densities from the spatial model when sterile moths are released. The two models yield the same result only if the nodes across the entire domain are homogenous with respect to initial infestation level, sterile release rate, cane variety and cane age.*

Diffusion on a homogenous domain with constant positive diffusion coefficients is expected to result in a gradual spreading over time. Spreading is expected to occur faster over time for higher values of $d(\underline{x})$. In order to verify whether the implementation of the dispersal process via constant diffusion responds as expected, the following simulations were performed with

$d(\underline{x}) \leq 0.2$:

1. *Initial infestation in $\mathcal{S}_p$ without sterile releases.* Initial infestation in $\mathcal{S}_p$ was set equal to 1 e/100s whereas initial infestation in $\mathcal{S}_{p'}$ was set equal to 0. Gradual spreading of *E. saccharina* occurred, with slower spreading over time for smaller diffusion coefficients (see Figure 5.6). The differences between neighbouring nodes tended to zero as t increased, which is expected for a model with positive diffusion coefficients. The model implementation, therefore, responds as expected when tested for its response to various diffusion coefficients.

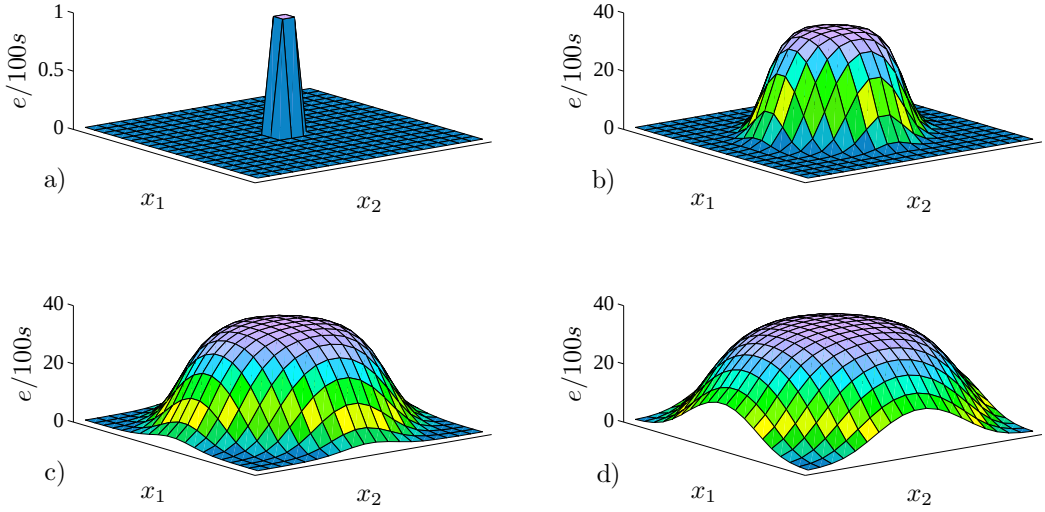


FIGURE 5.6: *Fertile moth population densities for different diffusion coefficients without sterile releases and initial infestation occurring in $\mathcal{S}_p$. (a) Moth population density at the beginning of the crop cycle, (b) moth population density at the end of the crop cycle with $d(x_1, x_2) = 0.005$, (c) moth population density at the end of the crop cycle with $d(x_1, x_2) = 0.015$, (d) moth population density at the end of the crop cycle with $d(x_1, x_2) = 0.025$.*

2. *Homogenous initial infestation with sterile releases in $\mathcal{S}_p$.* Initial infestation levels were homogenous across the entire domain and equal to 1 e/100s, with releases according to a ratio of 0.05 : 1 occurring only in $\mathcal{S}_p$ and zero release rates in $\mathcal{S}_{p'}$. Gradual spreading of sterile *E. saccharina* occurred which resulted in decreased larval and fertile moth population densities at nodes where sterile moths occurred, with slower spreading over time for smaller diffusion coefficients (see Figures 5.7 and 5.8). The differences between neighbouring nodes tended to zero as t increased, which is expected for a model with positive diffusion coefficients. The model implementation, therefore, responds as expected when tested for its response to various diffusion coefficients.

3. *Initial infestation in $\mathcal{S}_s > \mathcal{S}_{s'}$ without sterile releases.* Initial infestation levels in $\mathcal{S}_s$ were set equal to 2 e/100s, with initial infestation in $\mathcal{S}_{s'}$ equal to 1 e/100s. Gradual spreading of *E. saccharina* occurred from $\mathcal{S}_s$ to $\mathcal{S}_{s'}$, with slower spreading over time for smaller diffusion coefficients (see Figure 5.9). The differences between neighbouring nodes tended to zero as t increased, which is expected for a model with positive diffusion coefficients. The model implementation, therefore, responds as expected when tested for its response to various positive diffusion coefficients.

4. *Homogenous initial infestation with sterile releases in $\mathcal{S}_s$.* Initial infestation levels were homogenous across the entire domain and equal to 1 e/100s, with releases according to a

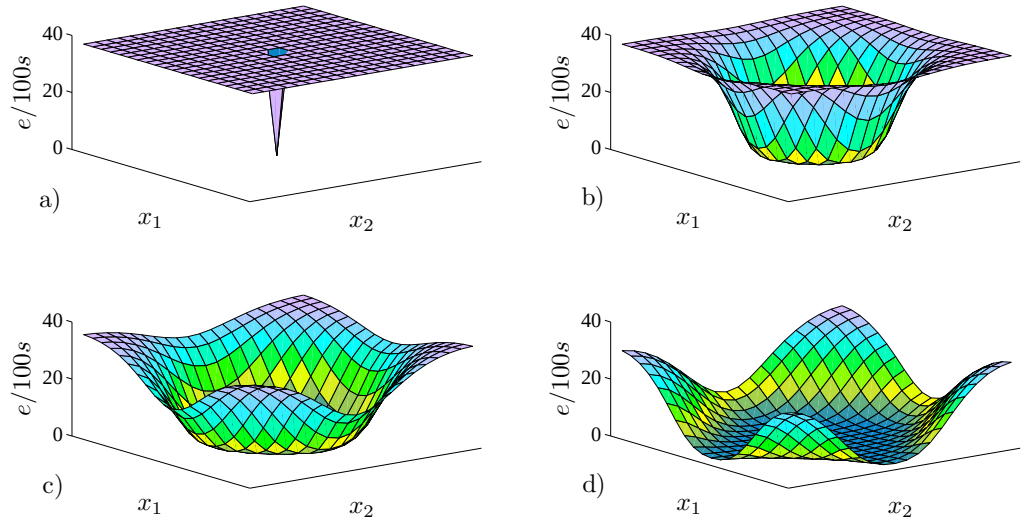


FIGURE 5.7: *Fertile moth population densities at the end of the crop cycle for different diffusion coefficients with homogenous initial infestation and sterile releases occurring in* $\mathcal{S}_p$. *(a)* $d(x_1, x_2) = 0$, *(b)* $d(x_1, x_2) = 0.05$, *(c)* $d(x_1, x_2) = 0.1$, *(d)* $d(x_1, x_2) = 0.15$.

ratio of 0.05 : 1 occurring only in $\mathcal{S}_s$ and zero release rates in $\mathcal{S}_{s'}$. Gradual spreading of sterile *E. saccharina* across $\mathcal{S}_{s'}$ occurred which resulted in decreased larval and fertile moth population densities at nodes where sterile moths occur, with slower spreading over time for smaller diffusion coefficients (see Figure 5.10). The differences between neighbouring nodes in $\mathcal{S}_s$ and $\mathcal{S}_{s'}$ tended to zero as t increased, which is expected for a model with positive diffusion coefficients. The model implementation, therefore, responds as expected when tested for its response to various diffusion coefficients.

5.6.2 Heterogeneous domain

A heterogeneous domain with respect to sugarcane variety and age is expected to result in heterogeneous infestation levels across $\mathcal{S}$. In patches where the cane variety is more susceptible or the crop is older, higher infestation levels are expected compared to patches with more resistant cane varieties and younger crops. However, as a result of dispersal, the infestation levels in patches where the cane variety is more resistant or the crop is younger will be higher than usual when it is adjacent to a field where the cane variety is more susceptible to *E. saccharina* infestation or where the crop is older. In order to verify whether the implementation of a heterogeneous domain with dispersal responds as expected, the following simulations were performed with $d(\underline{x}) \leq 0.2$:

1. *Variable mortality and no sterile releases.* Initial infestation levels and crop age were taken to be homogenous across the entire domain and equal to 1 e/100s. The cane variety was taken more resistant in $\mathcal{S}_s$ compared to the cane in $\mathcal{S}_{s'}$, therefore mortality was higher in $\mathcal{S}_s$ and infestation levels lower. Gradual spreading of *E. saccharina* occurred from $\mathcal{S}_{s'}$, where infestation levels were higher, to $\mathcal{S}_s$, which resulted in patches in $\mathcal{S}_s$ adjacent to patches in $\mathcal{S}_{s'}$ having higher infestation levels than patches in $\mathcal{S}_s$, which are further away from $\mathcal{S}_{s'}$. A slower spreading over time occurred for smaller diffusion coefficients, resulting in patches in $\mathcal{S}_s$ adjacent to patches in $\mathcal{S}_{s'}$ experiencing less increased infestation levels compared to infestation levels with larger diffusion coefficients (see Figure 5.11). The

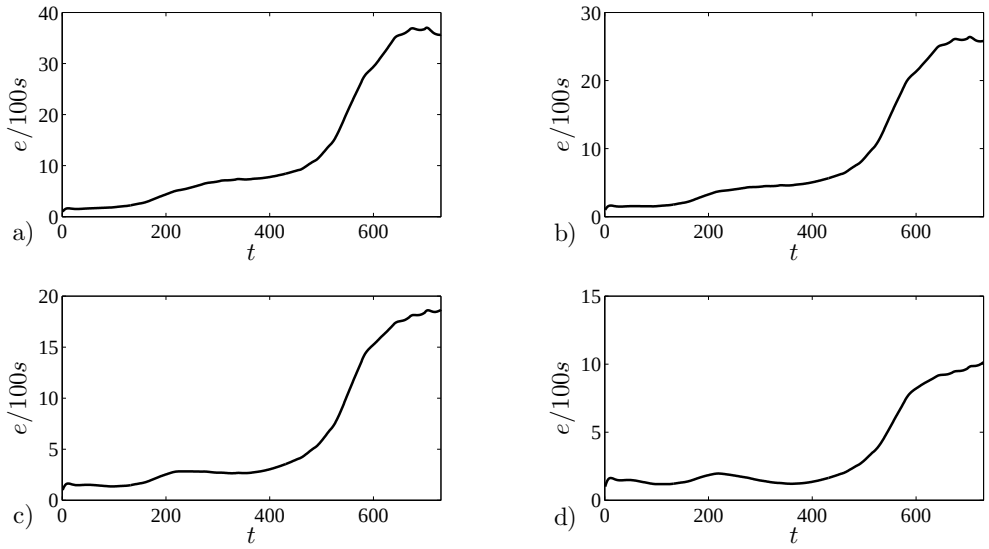


FIGURE 5.8: *Average larval population densities for different diffusion coefficients with sterile releases and initial infestation occurring in* $\mathcal{S}_p$. *(a)* $d(x_1, x_2) = 0$, *(b)* $d(x_1, x_2) = 0.05$, *(c)* $d(x_1, x_2) = 0.1$, *(d)* $d(x_1, x_2) = 0.15$.

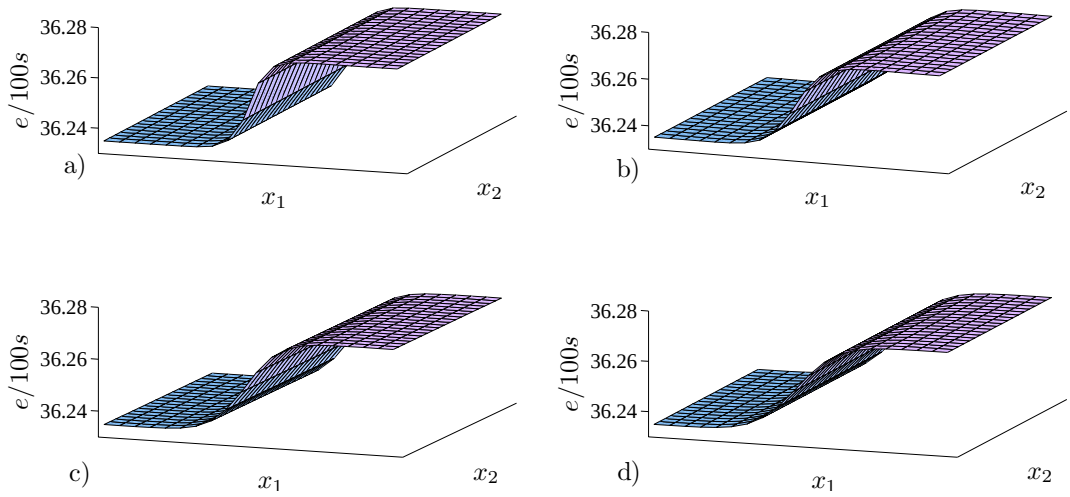


FIGURE 5.9: *Moth population densities at the end of the crop cycle for different diffusion coefficients without sterile releases and initial infestation in* $\mathcal{S}_s > \mathcal{S}_{s'}$. *(a)* $d(x_1, x_2) = 0.005$, *(b)* $d(x_1, x_2) = 0.01$, *(c)* $d(x_1, x_2) = 0.015$, *(d)* $d(x_1, x_2) = 0.02$.

model implementation, therefore, responds as expected when tested for its response to various diffusion coefficients.

2. *Variable cane age and no sterile releases.* Cane variety were taken to be homogenous across the entire domain. The crop in $\mathcal{S}_s$ was newly planted whereas the crop age in $\mathcal{S}_{s'}$ was equal to 12 months, therefore initial infestation levels was higher in $\mathcal{S}_{s'}$. Gradual spreading of *E. saccharina* occurred from $\mathcal{S}_{s'}$ to $\mathcal{S}_s$, which resulted in patches in $\mathcal{S}_s$ adjacent to patches in $\mathcal{S}_{s'}$ having higher infestation levels than patches in $\mathcal{S}_s$, which are further away from $\mathcal{S}_{s'}$. A slower spreading over time occurred for smaller diffusion coefficients, resulting in patches in $\mathcal{S}_s$ adjacent to patches in $\mathcal{S}_{s'}$ experiencing less increased infestation

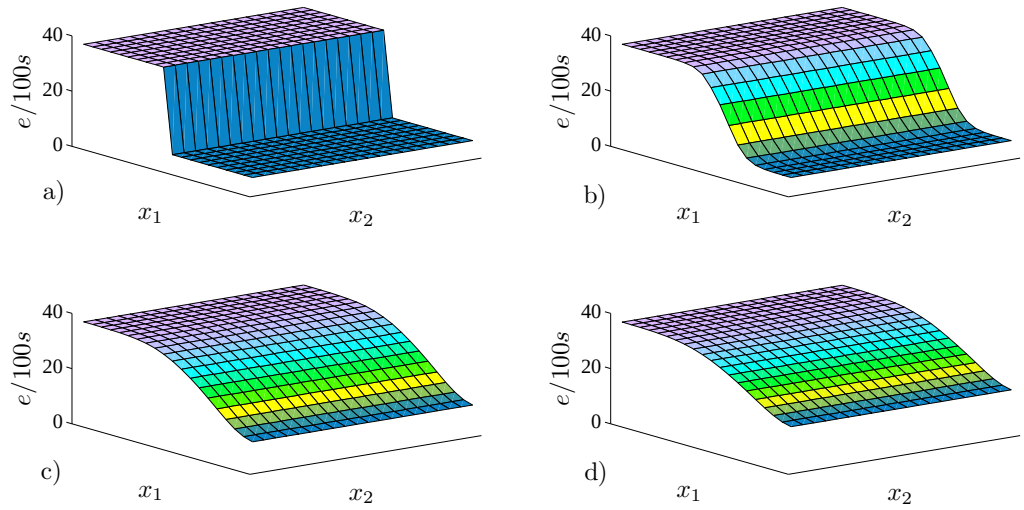


FIGURE 5.10: *Fertile moth population densities at the end of the crop cycle for different diffusion coefficients with a release ratio of* $0.05:1$ *in* $\mathcal{S}_s$. *(a)* $d(x_1, x_2) = 0$, *(b)* $d(x_1, x_2) = 0.05$, *(c)* $d(x_1, x_2) = 0.1$, *(d)* $d(x_1, x_2) = 0.15$.

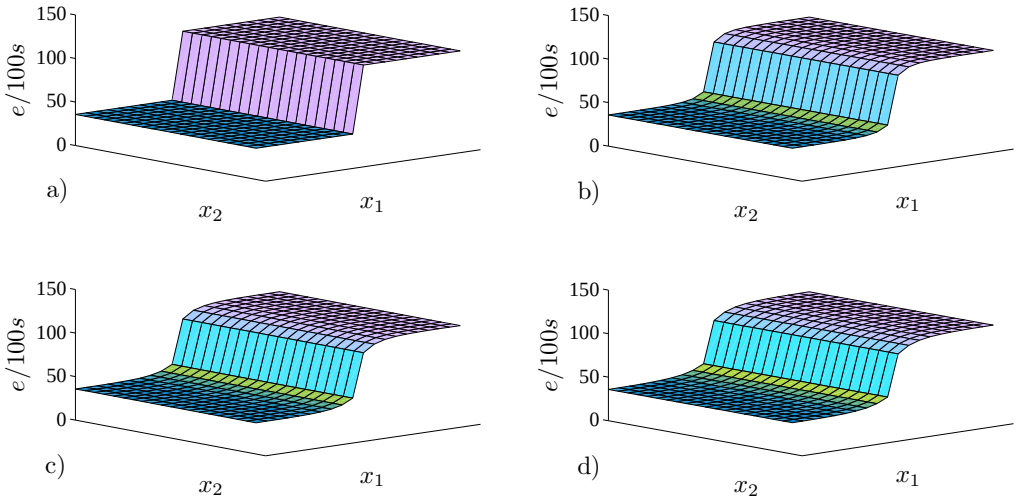


FIGURE 5.11: *Larval population densities at the end of the crop cycle on a heterogeneous domain (with respect to cane variety) for different diffusion coefficients. (a)* $d(x_1, x_2) = 0$, *(b)* $d(x_1, x_2) = 0.05$, *(c)* $d(x_1, x_2) = 0.1$, *(d)* $d(x_1, x_2) = 0.15$.

levels compared to infestation levels with larger diffusion coefficients (see Figure 5.12). The model implementation, therefore, responds as expected when tested for its response to various diffusion coefficients.

5.7 Numerical solution

Release strategies for different release scenarios have been obtained by means of simulations of the finite-difference approximation (5.7) implemented in MATLAB. Twice a week and weekly releases were shown in §4.8 to be the best release frequencies in terms of SIT profit and suppres-

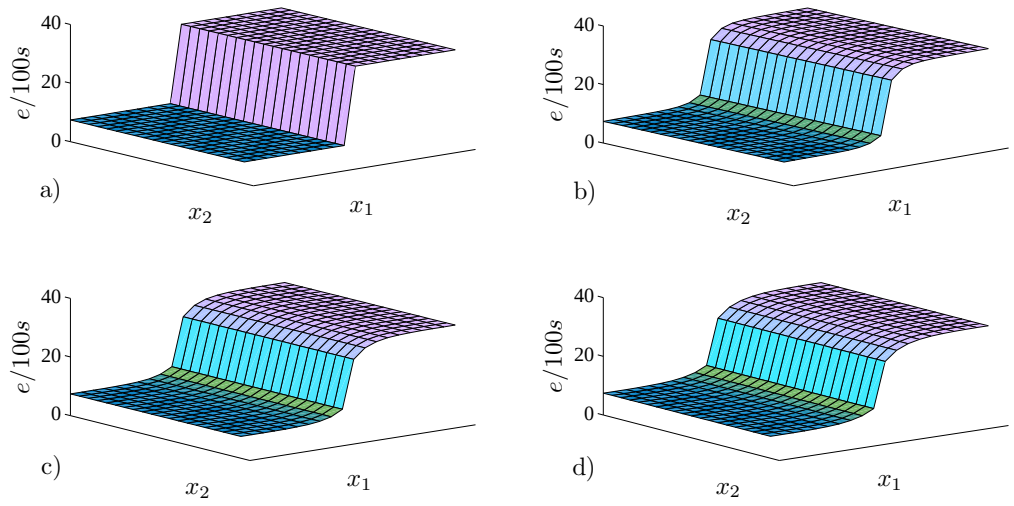


FIGURE 5.12: *Larval population densities after 12 months on a heterogeneous domain (with respect to crop age) for different diffusion coefficients. (a) $d(x_1, x_2) = 0$, (b) $d(x_1, x_2) = 0.05$, (c) $d(x_1, x_2) = 0.1$, (d) $d(x_1, x_2) = 0.15$.*

sion; therefore simulations in this chapter were only performed for $\theta = 3$ and $\theta = 7$. Simulations were performed for a homogenous field over a time period of 24 months for sugarcane planted in November, with a homogenous initial infestation of 0.1 e/100s. The fertile proportion of the F_1 generation of released sterile males was set equal to 0.1, the residual fertility in released moths was taken as 0, the male and female competitiveness were set at 1 and 0.1, respectively, sperm competitiveness was taken as 1, and sterile releases included both males and females. Growing conditions were assumed ideal, therefore the average stalk length on day t is given by (4.41), with a stalk height of approximately 1.4 m at maturation. Also, the density-dependent mortality function $b(t) = \frac{4}{(d^{2.5}+1)}$ was assumed.

For illustrative purposes, the cost per sterile insect (excluding labour and fuel costs) was assumed ranging between R0.03 and R0.10. For ATV releases, the labour cost per application was assumed R5, and the fuel cost was assumed R0.023 per 100m driven. For aerial releases, the labour and fuel cost combined was assumed R25 per hectare. The diffusion coefficient, $d(\underline{x})$, was assumed to be either 0.01 or 0.025. Simulations were performed for both a resistant ($\omega = 5$) and susceptible sugarcane variety ($\omega = 8$). Infestation and damage profiles for both types of varieties are shown in Figure 4.14. After 24 months, the resistant variety is expected to yield R62.24 for every patch of 25 m^2 (comprising a loss in revenue of 8.6% as a result of *E. saccharina* infestation), whereas the more susceptible variety is expected to yield R49.75/patch (comprising a loss in revenue of 27%).

5.7.1 ATV releases

SIT releases by means of ATVs may either result in a uniform distribution of sterile moths along the release lanes if mechanical release devices are used, or a discrete distribution of sterile moths along the release lanes at specific release points if releases are performed manually. Release lanes were assumed to range between 20 m and 50 m apart and release ratios were assumed to range between 0 and 150 : 1.

For releases performed twice a week, and $d(\underline{x}) = 0.025$, suppression below 1 e/100s was achieved

in the resistant variety when release lanes were at most 35 metres apart for manual releases (see Table 5.1), and at most 45 metres apart for releases with a mechanical device (see Table 5.2). If $d(\underline{x}) = 0.01$, suppression below 1 e/100s was achieved with release lanes at most 25 metres apart for manual releases, and at most 30 metres apart for mechanical releases (see Tables 5.1 and 5.2), but at much higher release ratios. The estimated decrease in damage levels with the corresponding increase in revenue for different release ratios is shown in Figures 5.13, 5.14, 5.15 and 5.16. From an economic point of view, for the assumed parameter values, only mechanical releases with release lanes at most 25 metres apart, $d(\underline{x}) = 0.025$ and $\kappa_r = 0.03$ appears to be a viable option for the resistant variety — suppression is achieved at a release ratio where the estimated increase in revenue is more than the SIT cost for the specific ratio. From §4.9 it is known that δ is more sensitive around η_{opt} than where $\eta > \eta_{opt}$. Therefore a value close to 10 : 1, where $I > C$, may be a good choice. If, for the assumed parameter values and $d(\underline{x}) = 0.025$, releases performed manually may be economically viable if release lanes are at most 25 m apart. However, in the sugarcane context, this may not always be possible.

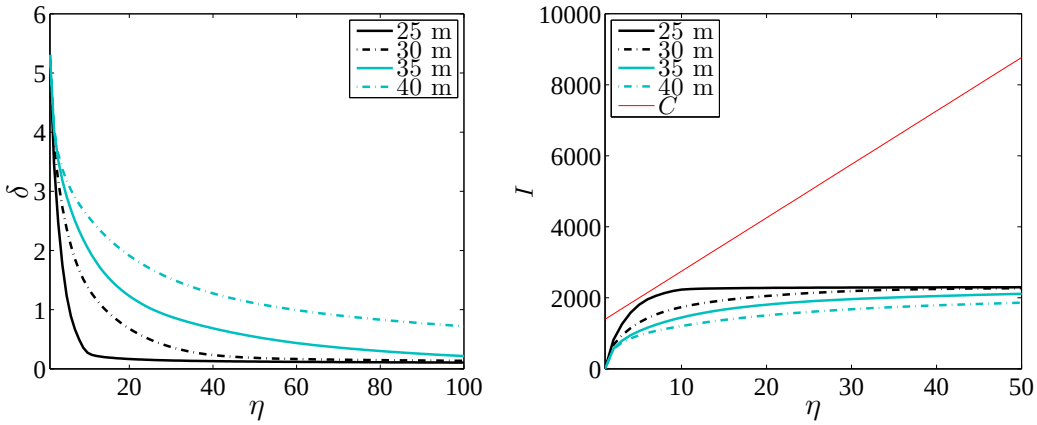


FIGURE 5.13: *The estimated percentage damage and increase in revenue for manual ATV releases performed twice a week with* $d(x_1, x_2) = 0.025$ *and* $\omega = 5$.

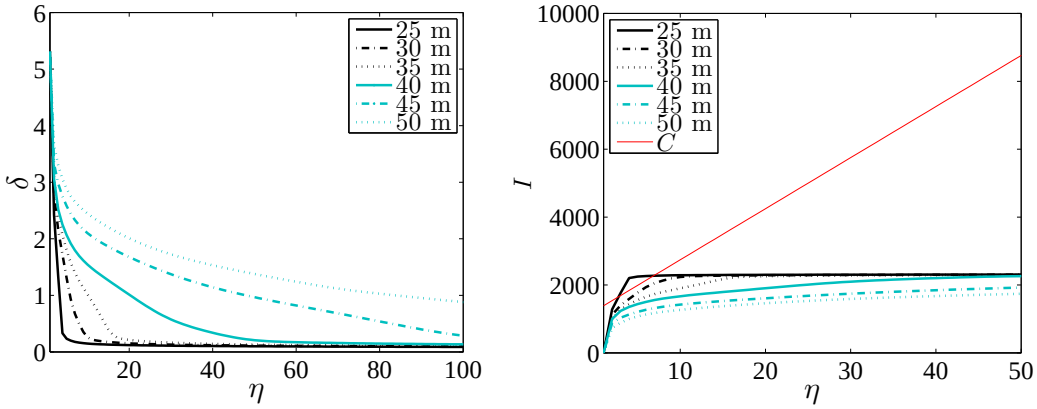


FIGURE 5.14: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed twice a week with* $d(x_1, x_2) = 0.025$ *and* $\omega = 5$.

For releases performed on a weekly basis, and $d(\underline{x}) = 0.025$, suppression below 1 e/100s was achieved in the resistant variety when release lanes were at most 30 metres apart for manual releases, and at most 40 metres apart for releases with a mechanical device. If $d(\underline{x}) = 0.01$, suppression below 1 e/100s was achieved with release lanes at most 20 metres apart for manual

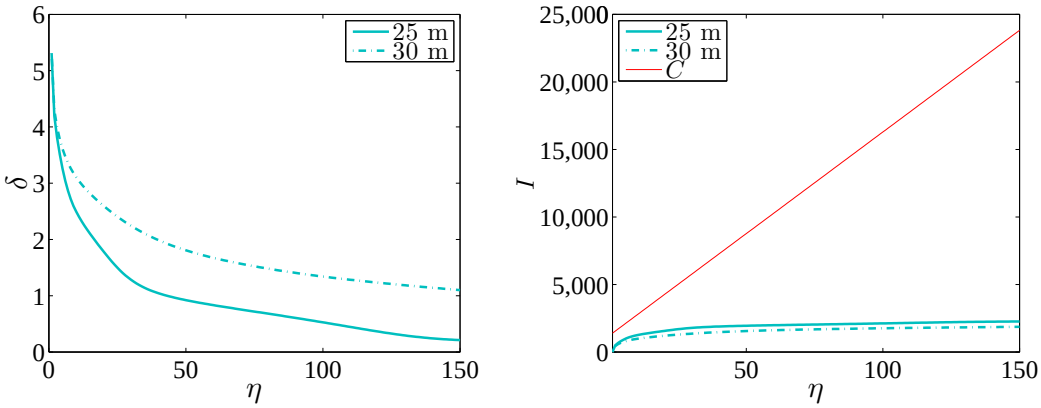


FIGURE 5.15: *The estimated percentage damage and increase in revenue for manual ATV releases performed twice a week with* $d(x_1, x_2) = 0.01$ *and* $\omega = 5$.

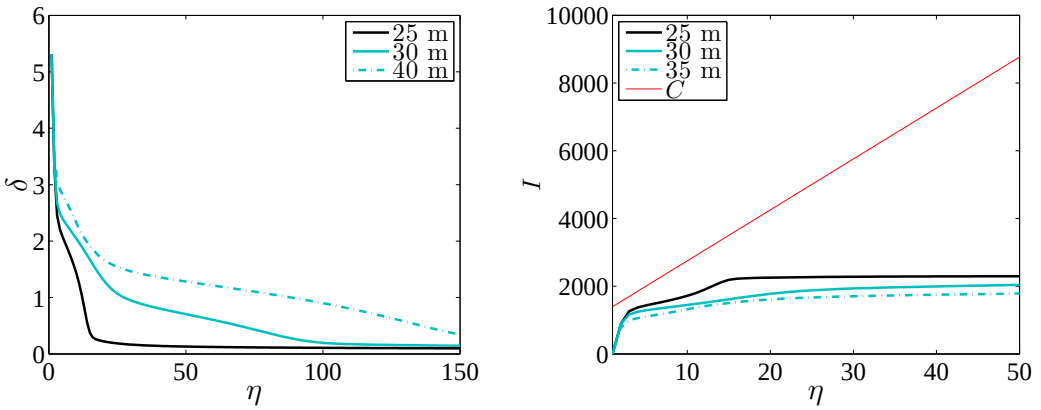


FIGURE 5.16: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed twice a week with* $d(x_1, x_2) = 0.01$ *and* $\omega = 5$.

releases, and at most 25 metres apart for mechanical device releases (see Tables 5.1 and 5.2). The estimated decrease in damage levels with the corresponding increase in revenue for different release ratios is shown in Figures 5.17, 5.18, 5.19 and 5.20. From an economical point of view, for the assumed parameter values, both manual and mechanical device releases with release lanes approximately 25 metres apart, $d(\underline{x}) = 0.025$ and $\kappa_r = 0.03$ appears to be a viable option for the resistant variety. Mechanical releases with release lanes up to 30 metres apart are economically viable. If $d(\underline{x}) = 0.01$, suppression may be obtained, but release ratios required for suppression result in $C > I$. In Figures 5.18 and 5.20, there appears to be economically viable ranges for the release ratio between 0 and 20 : 1 for release lanes more than 30 m apart (if $d(\underline{x}) = 0.025$) and 25 m or more apart (if $d(\underline{x}) = 0.01$). However, infestation levels at these release ratios are still more than 20 e/100s at the end of the sugarcane cycle — it is therefore not considered a viable solution in terms of suppression. If it is possible for release lanes to be between 15 m and 20 m apart for a given field layout and $d(\underline{x}) = 0.01$, an economically viable solution may be obtained for mechanical releases.

For releases performed twice a week, and $d(\underline{x}) = 0.025$, suppression below 1 e/100s was achieved in the susceptible variety when release lanes were at most 25 metres apart for manual releases, and at most 35 metres apart for releases with a mechanical device. If $d(\underline{x}) = 0.01$, suppression below 1 e/100s was achieved with release lanes at most 15 metres apart for manual releases, and at most 25 metres apart for releases with a mechanical device (see Tables 5.1 and 5.2). The

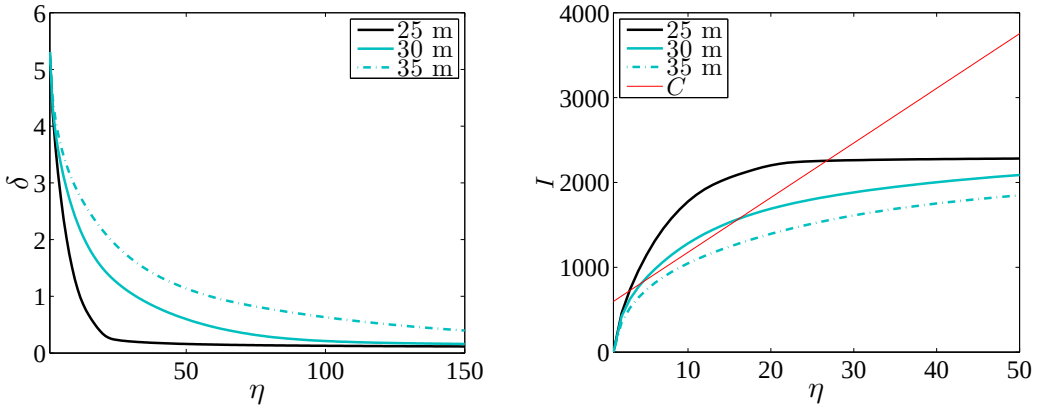


FIGURE 5.17: *The estimated percentage damage and increase in revenue for manual ATV releases performed weekly with* $d(x_1, x_2) = 0.025$ *and* $\omega = 5$.

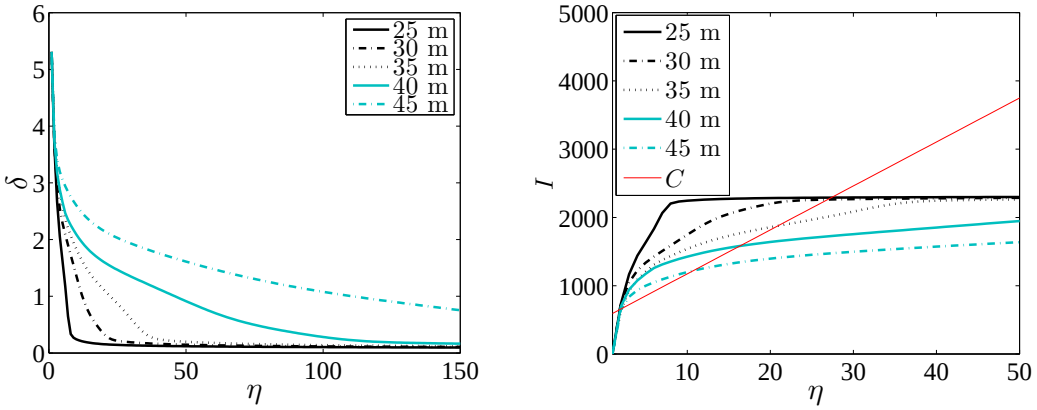


FIGURE 5.18: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed weekly with* $d(x_1, x_2) = 0.025$ *and* $\omega = 5$.

estimated decrease in damage levels with the corresponding increase in revenue for different release ratios is shown in Figures 5.21, 5.22, 5.23 and 5.24. Both manual and mechanical device releases with release lanes approximately 25 metres apart, $d(\underline{x}) = 0.025$ and $\kappa_r = 0.03$ appears to be a economically viable option for the susceptible variety. Mechanical releases with release lanes up to 30 m apart are economically viable. If $d(\underline{x}) = 0.01$, viable solutions were obtained at 15 m for manual releases and 20 m for mechanical releases.

If releases were performed on a weekly basis in the susceptible variety, and $d(\underline{x}) = 0.025$, suppression below 1 e/100s was achieved when release lanes were at most 25 metres apart for manual releases, and at most 35 metres apart for releases with a mechanical device. If $d(\underline{x}) = 0.01$, suppression below 1 e/100s was achieved with release lanes at most 15 metres apart for manual releases, and at most 25 metres apart for continuous releases (see Tables 5.1 and 5.2). The estimated decrease in damage levels with the corresponding increase in revenue for different release ratios is shown in Figures 5.25, 5.26, 5.27 and 5.28. Both manual and mechanical device releases with release lanes approximately 25 metres apart, $d(\underline{x}) = 0.025$ and $\kappa_r = 0.03$ appears to be an economically viable option for the susceptible variety. Mechanical releases with release lanes up to 30 m apart are economically viable. If $d(\underline{x}) = 0.01$, viable solutions were obtained at 15 m for manual releases and 20 m for mechanical releases.

Suppression of *E. saccharina* became extremely difficult for both the resistant and susceptible

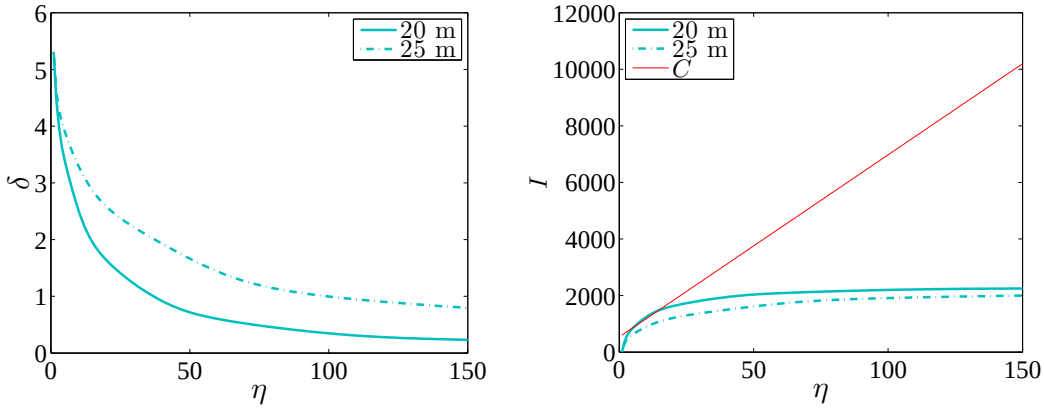


FIGURE 5.19: *The estimated percentage damage and increase in revenue for manual ATV releases performed weekly with* $d(x_1, x_2) = 0.01$ *and* $\omega = 5$.

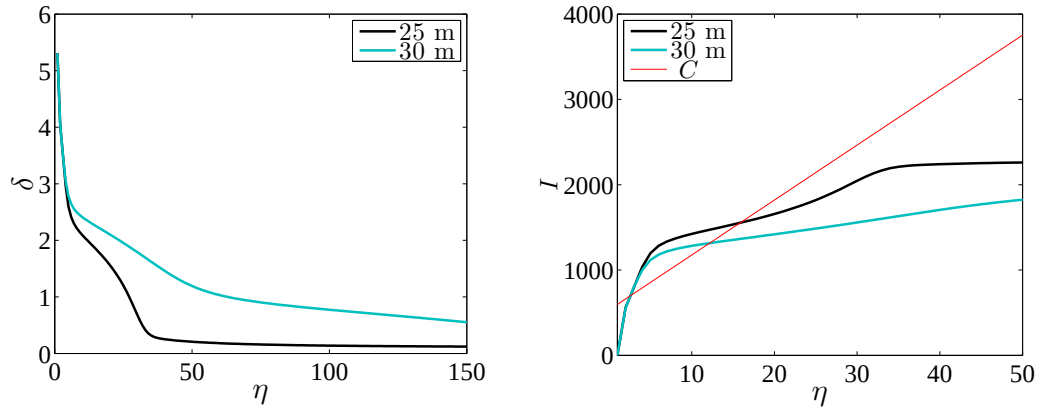


FIGURE 5.20: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed weekly with* $d(x_1, x_2) = 0.01$ *and* $\omega = 5$.

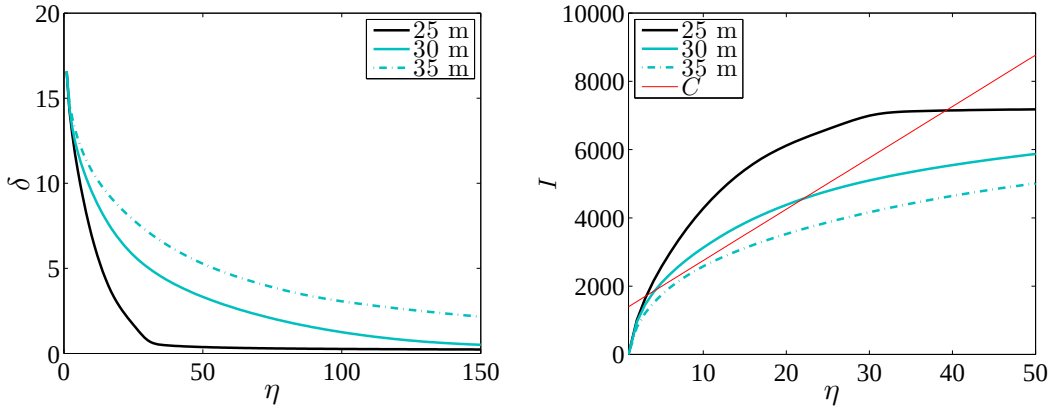


FIGURE 5.21: *The estimated percentage damage and increase in revenue for manual ATV releases performed twice a week with* $d(x_1, x_2) = 0.025$ *and* $\omega = 8$.

variety when release lanes were more than 40 m apart for both $d(\underline{x}) = 0.01$ and $d(\underline{x}) = 0.025$, with releases either twice a week or weekly. Suppression was achieved for all simulations when release lanes were 15 metres apart, and for most simulations when release lanes were 25 metres apart. Larger release ratios were necessary for suppression in the susceptible variety or when $d(\underline{x}) = 0.01$. Before considering manual or mechanical ATV releases, more research is required

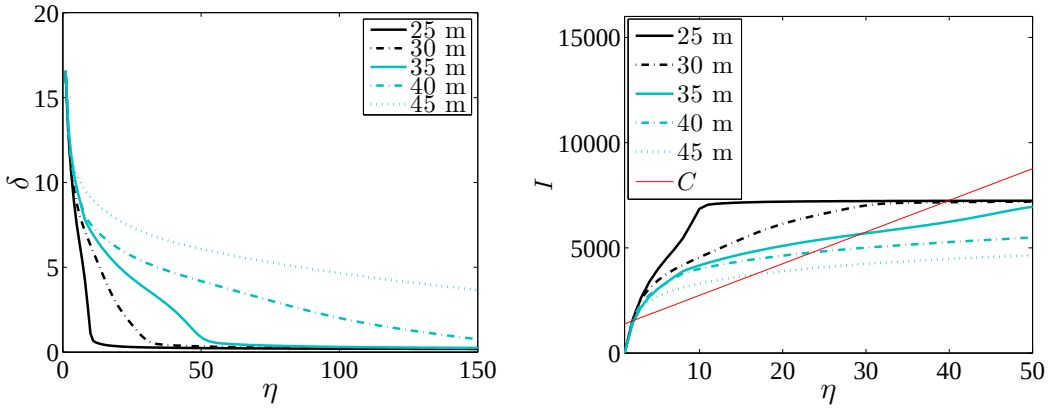


FIGURE 5.22: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed twice a week with* $d(x_1, x_2) = 0.025$ *and* $\omega = 8$.

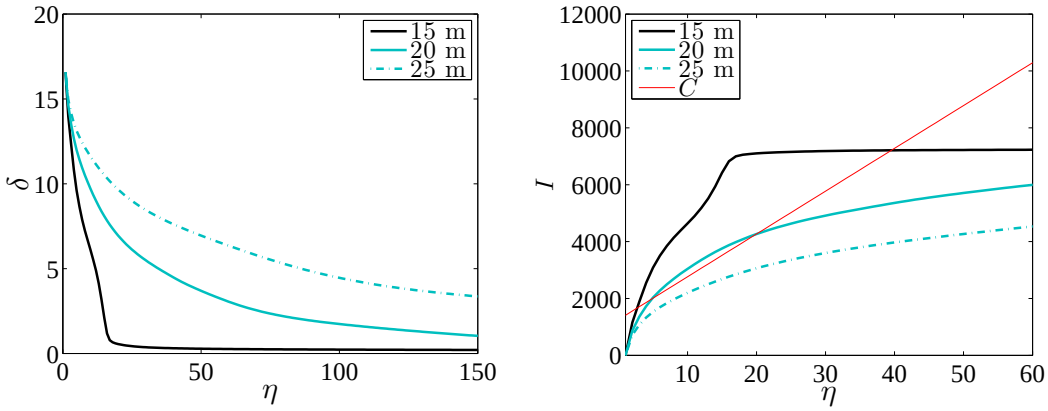


FIGURE 5.23: *The estimated percentage damage and increase in revenue for manual ATV releases performed twice a week with* $d(x_1, x_2) = 0.01$ *and* $\omega = 8$.

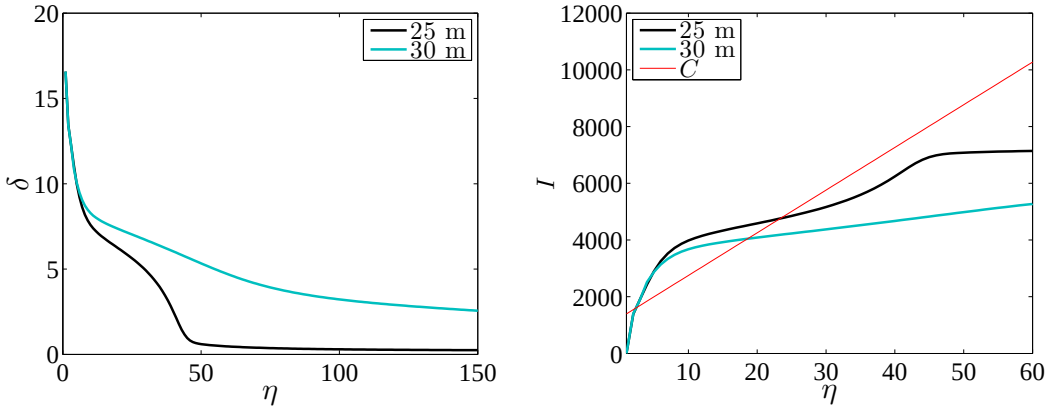


FIGURE 5.24: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed twice a week with* $d(x_1, x_2) = 0.01$ *and* $\omega = 8$.

with respect to the dispersal rates of *E. saccharina* moths within a sugarcane field in order to verify what the maximum distances between release lanes should be at which suppression may be achieved. Given the simulation results [85], twice a week releases are considered the best option in terms of risk (not obtaining suppression), whereas weekly releases are considered the best option in terms of SIT profit — suppression was achieved at smaller release ratios and

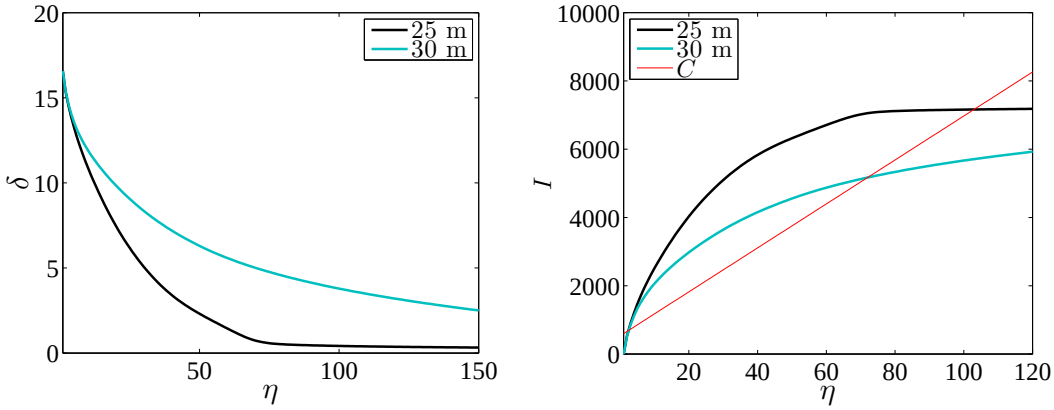


FIGURE 5.25: *The estimated percentage damage and increase in revenue for manual ATV releases performed weekly with* $d(x_1, x_2) = 0.025$ *and* $\omega = 8$.

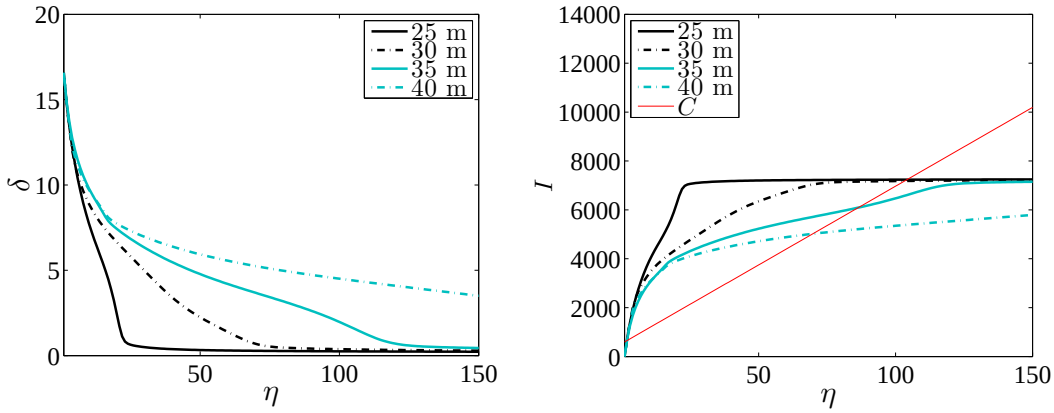


FIGURE 5.26: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed weekly with* $d(x_1, x_2) = 0.025$ *and* $\omega = 8$.

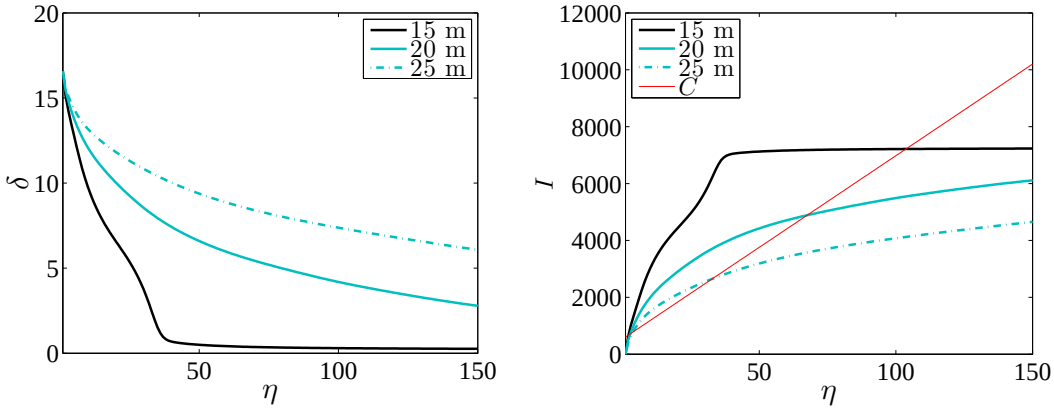


FIGURE 5.27: *The estimated percentage damage and increase in revenue for manual ATV releases performed weekly with* $d(x_1, x_2) = 0.01$ *and* $\omega = 8$.

larger distances between release lanes when releases were twice a week. However, SIT costs were much higher compared to weekly releases. Given a cost of $\kappa_r = 0.1$ per moth, $\kappa_\ell = 5$ per release and $\kappa_f = 0.023$ per 100 metres driven[3], in terms of SIT profit, ATV releases are not an

[3]The distance between release lanes does not contribute much towards the total release cost, since the fuel

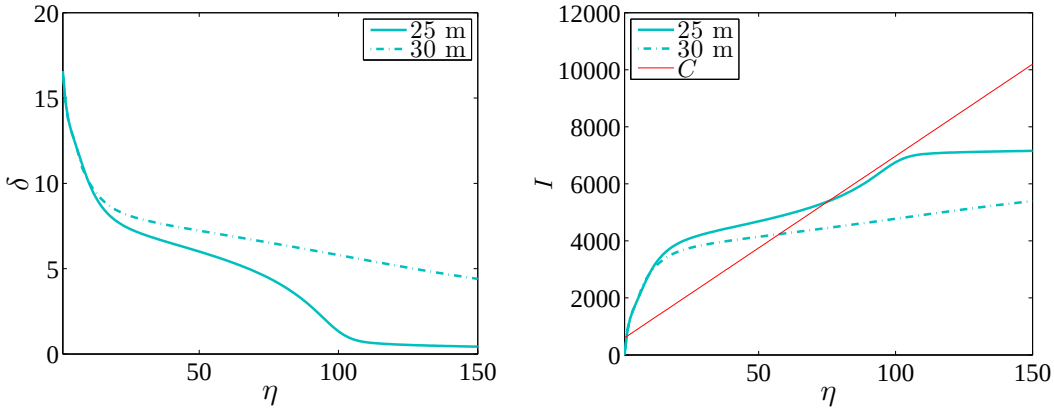


FIGURE 5.28: *The estimated percentage damage and increase in revenue for mechanical ATV releases performed weekly with* $d(x_1, x_2) = 0.01$ *and* $\omega = 8$.

economically viable strategy (see Tables 5.1 and 5.2). The costs involved in releasing moths at the high ratios required are, in most cases, much more than the increase in revenue estimated. If, however, $\kappa_r < 0.1$, ATV releases may be a viable release method to pursue[4]. Also, if only males were released, costs may be significantly lower (releasing only males would require more or less half the release ratio necessary for suppression compared to releasing both males and females — released sterile females do not contribute much towards suppression).

5.7.2 Aerial releases

SIT releases by means of an aircraft were simulated with release paths 100 metres apart during each release, and with released sterile moths Gaussian distributed across the areas underneath the flight paths. If released sterile moths disperse across a width of more than 100 m and the Gaussian distributions during subsequent releases overlap in such a way that a uniform distribution is a good approximation, the model described in Chapter 4 is applicable with a uniform distribution of released sterile insects. In this Chapter released sterile moths are, however, assumed to disperse across a width of at most 100 m (50 m in both directions) per release in order to obtain the smallest width of spread for which suppression may be obtained at release ratios smaller than 150 : 1. Simulations were performed for both the scenarios where the positions of the release lanes are static over time (referred to as a stationary aerial release distribution), and where the positions of the release lanes change over time (referred to as a non-stationary aerial release distribution).

Stationary aerial release distribution

Suppression below 5 e/100s was obtained in the resistant sugarcane variety when released moths spread from release lanes at least 90 m in the air before reaching the sugarcane canopy for both $d(\underline{x}) = 0.01$ and $d(\underline{x}) = 0.025$, with releases performed twice a week or weekly (see Tables 5.3 and 5.4).

consumption of ATVs is comparatively low and the amount of fuel used for the additional distances travelled due to extra release lanes is marginal.

[4]The cost to a farmer of applying SIT is currently estimated at between R0.03 and R0.06 per moth released in the codling and false codling moth SIT programmes [99, 120].

ω	θ	$\mathbf{d}(\underline{\mathbf{x}})$	**Distance apart**	η	**e/100s**	$\mathbf{P}_{\%}$ ($\kappa_r = 0.1$)	$\mathbf{P}_{\%}$ ($\kappa_r = 0.03$)
5	3	0.025	25	10:1	0.1	−17%	−2%
			30	43:1	0.2	−83%	−22%
			35	107:1	0.1	−212%	−61%
			40	150:1	3.9	−297%	−87%
		0.01	25	146:1	0.1	−291%	−84%
			30	150:1	9.6	−298%	−88%
	7	0.025	25	21:1	0.1	−12%	1%
			30	105:1	0.1	−84%	−20%
			35	150:1	2.2	−122%	−32%
		0.01	20	150:1	0.8	−122%	−32%
			25	150:1	6.6	−123%	−33%
8	3	0.025	25	33:1	0.1	−55%	5%
			30	150:1	1.3	−347%	−84%
		0.01	15	17:1	0.03	−14%	16%
			20	150:1	8.3	−348%	−85%
	7	0.025	25	76:1	0.1	−49%	8%
			30	150:1	25.3	−132%	−20%
		0.01	15	39:1	0.1	−10%	20%
			20	150:1	27.9	−133%	−21%

TABLE 5.1: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release (manual ATV releases). SIT costs of $\kappa_\ell = 5$ per hectare and $\kappa_f = 0.023$ per 100 m driven are assumed.*

For $d(\underline{x}) = 0.025$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 42 : 1$, with released moths spreading at least 90 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.01$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 125 : 1$, with released moths spreading at least 90 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.025$ and with releases performed weekly, suppression below 1 e/100s was achieved at $\eta = 95 : 1$, with released moths spreading at least 90 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.01$ and with releases performed weekly, suppression below 5 e/100s was achieved at $\eta = 150 : 1$, with released moths spreading at least 90 metres before reaching the sugarcane canopy. The smaller the dispersal coefficient, the more difficult it is to achieve suppression, since the number of released moths dispersing to the endpoints of the distribution is smaller — therefore much larger release ratios are necessary in order to achieve suppression (see Figure 5.29). Also, with releases performed weekly, suppression was achieved at larger release ratios; weekly releases, however, have the advantage of lower SIT costs (see Figures 4.26 and 4.27).

Suppression below 1 e/100s was achieved in the susceptible sugarcane variety when released moths spread from release lanes at least 90 m in the air before reaching the sugarcane canopy for both $d(\underline{x}) = 0.01$ and $d(\underline{x}) = 0.025$, with releases performed twice a week or weekly (see Tables 5.5 and 5.6).

For $d(\underline{x}) = 0.025$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 130 : 1$, with released moths spreading at least 90 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.01$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 26 : 1$, with released moths spreading at least 100 metres

ω	θ	$\mathbf{d}(\underline{\mathbf{x}})$	**Distance apart**	η	**e/100s**	$\mathbf{P}_{\%}$ ($\kappa_r = 0.1$)	$\mathbf{C}_{\%}$ ($\kappa_r = 0.03$)
5	3	0.025	25	4:1	0.1	−3%	2%
			30	10:1	0.2	−17%	−2%
			35	16:1	0.1	−29%	−6%
			40	49:1	0.1	−95%	−26%
			45	109:1	0.1	−214%	−62%
			50	150:1	4.5	−298%	−87%
		0.01	25	15:1	0.1	−27%	−5%
			30	100:1	0.1	−198%	−56%
			35	150:1	1	−297%	−87%
	7	0.025	25	7:1	0.1	0.4%	5%
			30	22:1	0.1	−12%	1%
			35	37:1	0.1	−25%	−3%
			40	115:1	0.1	−92%	−23%
			45	150:1	6.6	−123%	−33%
		0.01	25	35:1	0.1	−24%	−2%
			30	150:1	4.7	−122%	−32%
8	3	0.025	25	10:1	0.05	3%	22%
			30	33:1	0.1	−54%	5%
			35	55:1	0.1	−110%	−12%
			40	150:1	4.25	−354%	−91%
		0.01	25	48:1	0.1	−93%	−7%
			30	150:1	24.6	−351%	−88%
	7	0.025	25	23:1	0.1	8%	25%
			30	77:1	0.1	−50%	8%
			35	127:1	0.1	−104%	−8%
			40	150:1	36.3	−135%	−22%
		0.01	25	111:1	0.1	−87%	−3%
			30	150:1	46.7	−137%	−24%

TABLE 5.2: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release (mechanical ATV releases). SIT costs of $\kappa_\ell = 5$ per ha and $\kappa_f = 0.023$ per 100 m driven are assumed.*

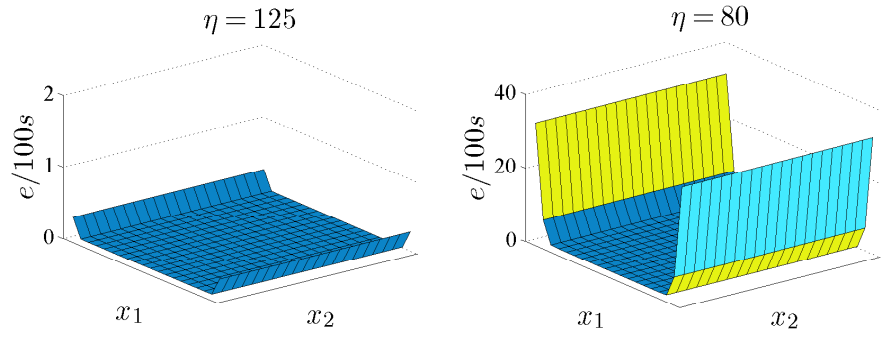


FIGURE 5.29: *Larval population density in a 1 hectare field with aerial releases at different ratios and $d(x_1, x_2) = 0.01$.*

before reaching the sugarcane canopy. For $d(\underline{x}) = 0.025$ and with releases performed weekly, suppression below 1 e/100s was achieved at $\eta = 50 : 1$, with released moths spreading at least

Spread	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$			
	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$	
80	150:1	3.7	−299%	150:1	3.7	−299%	3539%
90	125:1	0.2	−250%	42:1	0.1	−83%	1003%
100	8:1	0.1	−15%	6:1	0.1	−11%	217%

TABLE 5.3: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for aerial releases performed twice a week with* $\omega = 5$. *SIT costs of* $\kappa_r = 0.1$ *and* $\kappa_\ell + \kappa_f = 5.8$ *are assumed.*

Spread	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$		
	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$
80	150:1	6.6	−124%	150:1	3.7	−123%
90	150:1	4.3	−123%	95:1	0.1	−76%
100	21:1	0.1	−12%	15:1	0.3	−6%

TABLE 5.4: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for aerial releases performed weekly with* $\omega = 5$. *SIT costs of* $\kappa_r = 0.1$ *and* $\kappa_\ell + \kappa_f = 5.8$ *are assumed.*

100 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.01$ and with releases performed weekly, suppression below 1 e/100s was achieved at $\eta = 64 : 1$, with released moths spreading at least 100 metres before reaching the sugarcane canopy.

As may be seen from Tables 5.3, 5.4, 5.5 and 5.6, SIT costs outweigh the estimated increase in revenue if $\kappa_r = 0.1$ and $\kappa_\ell + \kappa_f = 5.8$, even if released moths spread across 100 m during release. If, however, $\kappa_r < 0.1$ aerial releases may be a viable release method in terms of profit (see Figures 5.30 and 5.31) for small enough release ratios. In terms of both profit and suppression, it may only be a viable release method if $d(\underline{x}) > 0.01$ and releases are performed weekly for the resistant sugarcane variety, and either twice a week or weekly for the susceptible sugarcane variety.

Spread	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$		
	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$
90	150:1	16	−352%	130:1	0.1	−301%
100	26:1	0.1	−39%	20:1	0.2	−24%

TABLE 5.5: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for aerial releases performed twice a week with* $\omega = 8$. *SIT costs of* $\kappa_r = 0.1$ *and* $\kappa_\ell + \kappa_f = 5.8$ *are assumed.*

Non-stationary aerial release distribution

Simulations for non-stationary aerial release distributions were also performed. The non-stationary aerial release distributions were obtained by alternating two different stationary release distributions, each with release paths 100 metres apart but with a 50 metre difference between the alternate release paths, at each consecutive release. The alternating stationary release distributions, each having released moths spread according to a Gaussian distribution along the release paths, may overlap such that, after two release periods, a close-to-uniform dis-

Spread	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$		
	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$
90	150:1	20.8	−133%	150:1	19.9	−132%
100	64:1	0.1	−37%	50:1	0.1	−22%

TABLE 5.6: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for aerial releases performed weekly with $\omega = 8$. SIT costs of $\kappa_r = 0.1$ and $\kappa_\ell + \kappa_f = 5.8$ are assumed.*

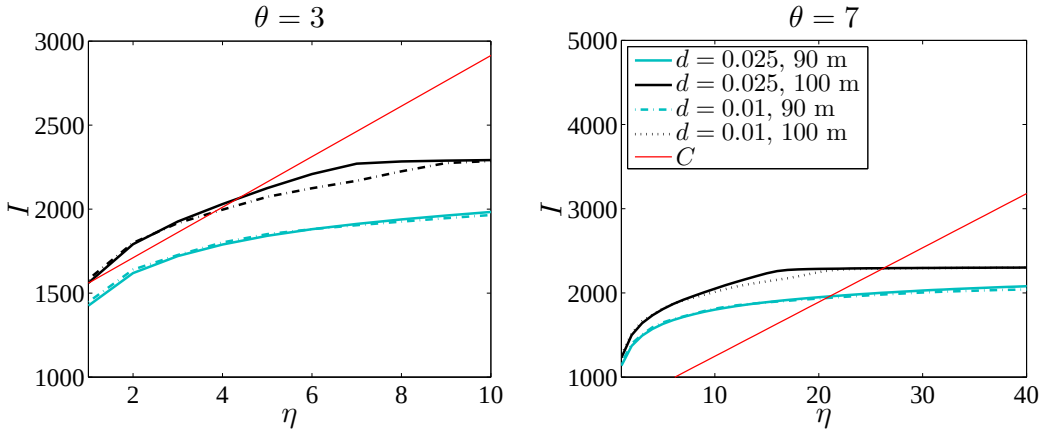


FIGURE 5.30: *Comparison between the estimated increase in revenue and SIT costs at different release ratios for aerial releases performed twice a week or weekly in the resistant sugarcane variety. SIT costs of $\kappa_r = 0.03$ and $\kappa_\ell + \kappa_f = 5.8$ are assumed.*

tribution of released moths is obtained. This, however, depends on the width of the Gaussian distributions (how far the released moths spread along the release paths), and the frequency of the releases, since moths have a short lifespan of approximately 5 days.

Suppression below 1 e/100s was obtained in the resistant sugarcane variety when released moths spread from release lanes at least 40 m in the air before reaching the sugarcane canopy for both $d(\underline{x}) = 0.01$ and $d(\underline{x}) = 0.025$, with releases performed twice a week or weekly (see Tables 5.7 and 5.8).

Spread	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$		
	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$
10	150:1	16.7	−90%	114:1	0.9	−64%
20	150:1	15.9	−90%	104:1	0.9	−58%
30	150:1	9.3	−89%	46:1	0.9	−25%
40	61:1	0.8	−34%	15:1	0.03	−0.06%
50	7:1	0.002	−0.01%	4:1	0.004	0.01%
60	2:1	0.001	2%	2:1	0.001	2%
100	1:1	0.001	3%	1:1	0.001	3%

TABLE 5.7: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for non-stationary aerial releases performed twice a week with $\omega = 5$. SIT costs of $\kappa_r = 0.03$ and $\kappa_\ell + \kappa_f = 5.8$ are assumed.*

For $d(\underline{x}) = 0.025$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 114 : 1$, with released moths spreading at least 10 metres before reaching

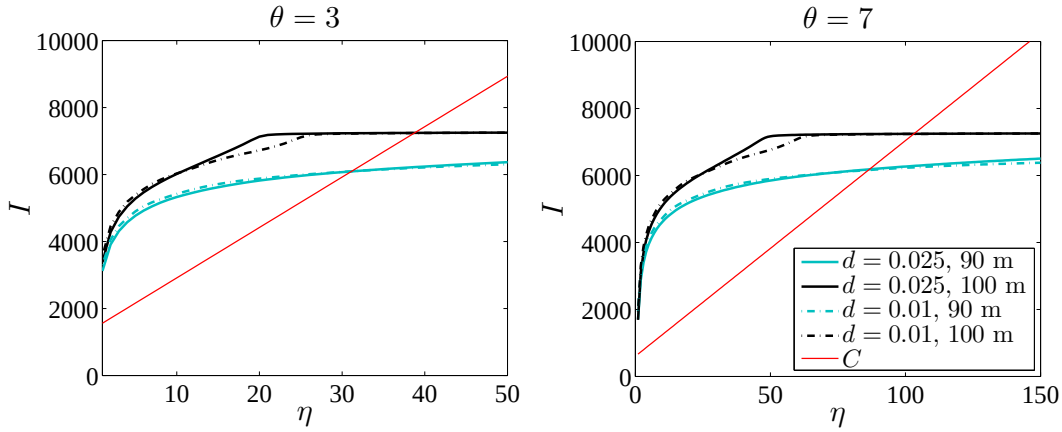


FIGURE 5.31: *Comparison between the estimated increase in revenue and SIT costs at different release ratios for aerial releases performed twice a week or weekly in the susceptible sugarcane variety. SIT costs of* $\kappa_r = 0.03$ *and* $\kappa_\ell + \kappa_f = 5.8$ *are assumed.*

	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$		
Spread	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$
20	150:1	18.23	−35%	150:1	7.2	−33%
30	150:1	12	−34%	108:1	0.9	−21%
40	143:1	0.9	−30%	34:1	0.6	−2%
50	16:1	0.1	2.5%	9:1	0.1	4%
60	5:1	0.001	5%	4:1	0.001	5.5%
100	1:1	0.005	6%	1:1	0.001	6%

TABLE 5.8: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for non-stationary aerial releases performed weekly with* $\omega = 5$. *SIT costs of* $\kappa_r = 0.03$ *and* $\kappa_\ell + \kappa_f = 5.8$ *are assumed.*

the sugarcane canopy. At a 10 metre spread, and therefore 45 metres between the tails of the alternating release distributions, releases are almost similar to ATV releases with release lanes 45 metres apart. The results are consistent with the results from ATV releases, where suppression was achieved at $\eta = 109:1$ for release lanes 45 metres apart. For $d(\underline{x}) = 0.01$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 61:1$, with released moths spreading at least 40 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.025$ and with releases performed weekly, suppression below 1 e/100s was achieved at $\eta = 108:1$, with released moths spreading at least 30 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.01$ and with releases performed weekly, suppression below 1 e/100s was achieved at $\eta = 143:1$, with released moths spreading at least 40 metres before reaching the sugarcane canopy.

Suppression below 1 e/100s was achieved in the susceptible sugarcane variety when released moths spread in release lanes at least 50 m in the air before reaching the sugarcane canopy for both $d(\underline{x}) = 0.01$ and $d(\underline{x}) = 0.025$, with releases performed twice a week or weekly (see Tables 5.9 and 5.10).

For $d(\underline{x}) = 0.025$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 45:1$, with released moths spreading at least 40 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.01$ and with releases performed twice a week, suppression below 1 e/100s was achieved at $\eta = 18:1$, with released moths spreading at least 50 metres

Spread	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$		
	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$
30	150:1	49	−94%	150:1	2.4	−85%
40	150:1	22	−88%	45:1	0.8	−53%
50	18:1	0.03	15%	11:1	0.02	21%
60	5:1	0.03	25%	4:1	0.007	26%
100	1:1	0.23	27%	1:1	0.02	27%

TABLE 5.9: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for non-stationary aerial releases performed twice a week with* $\omega = 8$. *SIT costs of* $\kappa_r = 0.03$ *and* $\kappa_\ell + \kappa_f = 5.8$ *are assumed.*

Spread	$\mathbf{d(\underline{x}) = 0.01}$			$\mathbf{d(\underline{x}) = 0.025}$		
	η	e/100s	$P_{\%}$	η	e/100s	$P_{\%}$
30	150:1	58	−29%	150:1	41	−23%
40	150:1	33	−22%	106:1	0.9	−2%
50	45:1	0.4	18%	26:1	0.2	24%
60	13:1	0.01	29%	10:1	0.01	30%
100	3:1	0.001	32%	3:1	0.001	32%

TABLE 5.10: *Comparison between release ratios, infestation levels at the end of the sugarcane cycle, increase in revenue estimated and the cost of release for non-stationary aerial releases performed weekly with* $\omega = 8$. *SIT costs of* $\kappa_r = 0.03$ *and* $\kappa_\ell + \kappa_f = 5.8$ *are assumed.*

before reaching the sugarcane canopy. For $d(\underline{x}) = 0.025$ and with releases performed weekly, suppression below 1 e/100s was achieved at $\eta = 106 : 1$, with released moths spreading at least 40 metres before reaching the sugarcane canopy. For $d(\underline{x}) = 0.01$ and with releases performed weekly, suppression below 1 e/100s was achieved at $\eta = 45 : 1$, with released moths spreading at least 50 metres before reaching the sugarcane canopy.

In accordance with the simulation results for stationary aerial release distributions, the smaller the dispersal coefficient, the more difficult it is to achieve suppression — much larger release ratios are required. Also, with releases performed weekly, suppression was achieved at larger release ratios; however, weekly releases have the advantage of lower SIT costs. As may be seen from Tables 5.7, 5.8, 5.9 and 5.10, economically viable release strategies exist if $\kappa_r = 0.03$ and $\kappa_\ell + \kappa_f = 5.8$, depending on how far the released moths spread before reaching the sugarcane canopy. For values greater than $\kappa_r = 0.03$ or $\kappa_{ell} + \kappa_f = 5.8$, or if the initial infestation is higher than 0.1 e/100s, economically viable strategies may exist for small release ratios. A small increase in the cost per sterile moth, labour cost or initial infestation, however, results in the SIT cost outweighing the estimated increase in revenue (see Figure 5.32). From simulation results of stationary aerial release distributions, it was established that for $\kappa_r = 0.10$, no economic viable strategies exist at the release ratios required for suppression.

It is also clear from the simulations results that non-stationary aerial releases perform better than stationary aerial releases — moths are not required to spread so far before reaching the sugarcane canopy as with stationary aerial releases. Also, alternating between two or more release distributions may result in a close to uniform distribution of released moths. The release ratio required for suppression at a close-to-uniform release distribution is below 10:1, resulting in a more effective and less costly release strategy. Before considering aerial releases, however,

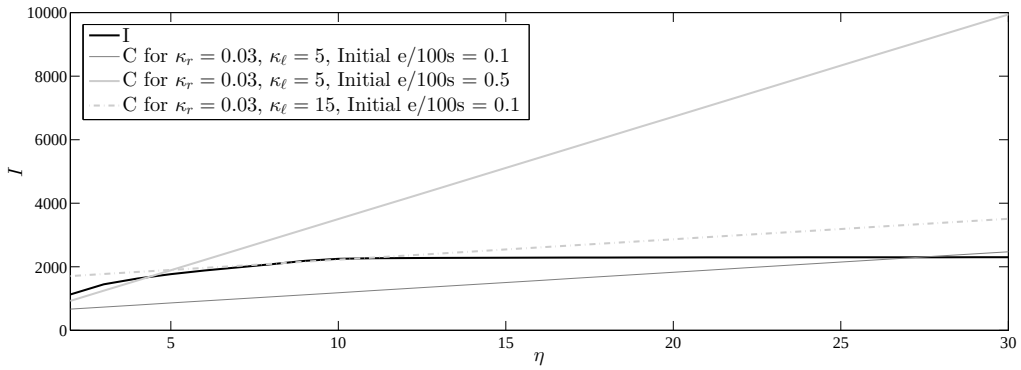


FIGURE 5.32: *Comparison between the estimated increase in revenue and SIT costs for a resistant sugarcane variety with different values of κ_r, $\kappa_\ell + \kappa_f$ and initial infestation levels. Moths are assumed to spread 50 metres in the air before reaching the sugarcane canopy, and release lanes are non-stationary.*

more research is required with respect to the dispersal rates of *E. saccharina* moths within a sugarcane field, and also how far they actually disperse while being released from an aircraft before reaching the canopy. If moths do not disperse over a very wide range before reaching the canopy, it may be worth considering release flight paths less than 100 metres apart. However, this will increase the release cost due to the increased fuel consumption per hectare.

5.7.3 Heterogeneous domain

If, for example, a field containing a resistant variety is next to a field containing a susceptible variety, it may be seen from §5.6.2, for the assumed range of $d(\underline{x})$, that the higher infestation in the one field only affects the patches nearby the edges of the different fields as a result of dispersal between the fields. It is therefore expected that, for a heterogeneous domain, the numerical solutions obtained in §5.7 are still applicable for each field in the domain, respectively, with only marginal changes in the release ratio required for suppression in each field. An example scenario of such a heterogeneous domain is discussed in detail in the next chapter, together with the corresponding release distributions and ratios required for suppression.

5.8 Model validation

E. saccharina growth without sterile releases on a homogenous domain was shown in §4.7 to be adequately represented by the reaction terms of the spatio-temporal model. In contrast with the mean-field model described in Chapter 4, the spatio-temporal model of this chapter does not assume 'global' migration. Therefore it is possible to assume different spatial distributions of released sterile moths in the latter model, which may be more realistic in the given context. The mean-field model is only realistic for uniform distributions across the spatial domain, which may only be obtained if releases are from an aircraft, with flight paths not too far apart. The release ratios estimated in §5.7 compare favourably to current SIT projects where release ratios of at least 10:1 are pursued [1, 35, 51, 99, 120] for ATV releases in release lanes between 24 m and 32 m apart [120]. As mentioned in §4.7, in the context of a sugarcane farm, a number of sugarcane varieties may be planted on different fields, all having different ages and therefore different harvesting times. If the environment is heterogeneous, the population growth and distribution of *E. saccharina* cannot be described by the mean-field approximation and needs to be modelled as a function of both time and space, as in the case of the spatio-temporal

model of this chapter. The spatio-temporal model is therefore considered a more valid model for describing different types of sterile releases and *E. saccharina* growth and interaction with released sterile insects on a heterogeneous spatial domain.

5.9 Sensitivity Analysis

The spatio-temporal model assumes the same reaction terms and parameters in (5.1) compared to the mean-field model (4.1). Hence a sensitivity analysis with respect to growth, mortality, maturation and SIT parameters is expected to yield the same results as those of the mean-field model. Numerical analyses of the spatio-temporal model were performed in §5.7 with the diffusion coefficient varied within the assumed range of $d(\underline{x})$, which shows how the spatio-temporal model reacts with respect to changes in $d(\underline{x})$ and different spatial distributions of released sterile moths. A sensitivity analysis of the spatio-temporal model was therefore deemed unnecessary.

5.10 Chapter summary

A detailed description of the *E. saccharina* model in a spatially and temporally variable environment was presented in §5.3, along with the underlying assumptions made in §5.2. The mean-field model of Chapter 4 was extended to a spatially explicit model with local dispersal between neighbouring habitats in order to investigate the effect of dispersal on SIT. The spatio-temporal model comprises a discrete reaction-diffusion system with zero-flux Neumann boundary conditions and initial values obtained from simulations of the mean-field model of Chapter 4.

In §5.4 the diffusion coefficients, release methods and the changes in parameters according to a heterogeneous environment were considered. In §5.6, simulations were performed in order to verify whether the implementation of the model represents a correct representation of the logic contained in the mathematical description of the model. The model implementation responded as expected to changes in all parameters, thereby verifying the model. The model was also validated in §5.8 by means of data obtained from similar SIT projects.

Numerical results of the model for different release methods were presented in §5.7. Twice a week releases were found to be the best option in terms of risk (not achieving suppression), whereas weekly releases were found to be the best option in terms of SIT profit — suppression may be achieved at smaller release ratios and larger distances between release lanes when releases were twice a week; however, SIT costs were much higher compared to weekly releases. The maximum distance between ATV release lanes was estimated to range between 15 m and 30 m, depending on the release method, frequency and dispersal rate. Also, in terms of SIT profit, for the release ratios estimated, the cost per sterile insect should satisfy $\kappa_r < 0.1$, in order to obtain an economically viable strategy. Aerial releases, with currently used aircraft are not considered viable in terms of cost (for flight paths spaced 100 m apart, $\kappa_\ell + \kappa_f >$R20 per hectare). However, if application costs for UAVs are significantly lower, aerial releases may be considered. Non-stationary aerial release distributions performed better than stationary aerial release distributions — suppression was obtained with moths spreading between 10 metres and 50 metres, compared to 90 metres for stationary distributions. In §5.8 the model results were compared with the practices in other SIT projects. The release ratios and distances between release lanes compare well with those adopted in other SIT projects in South Africa.

CHAPTER 6

SIT simulation tool

Contents

"Appearance is something absolute, but reality is not that way - everything is interdependent, not absolute."
— Dalai Lama

The focus in this chapter turns away from developing suitable mathematical models, such as the ones described in Chapters 4 and 5, and moves towards the implementation of a user-friendly simulation tool. The objective is to introduce a basic platform whereby the effectiveness of SIT may be investigated in different scenarios, depending on various parameter values and spatial domains. In addition, the workability of the spatio-temporal model of Chapter 5, when applied to different heterogeneous domains, including realistic sugarcane field layouts, is illustrated. The simulation tool includes a graphical user interface and is extended to include the handling of GIS[1] shapefiles[2] representing realistic sugarcane farm layouts. The tool may eventually be extended to a DSS for use in an AW-IPM programme. The design and working of the computerised platform is described in this chapter, along with the difficulties encountered in applying the spatio-temporal model to a real-life scenario and the assumptions made to overcome them. A case study of a realistic SIT scenario is also presented along with the numerical results obtained.

[1] A geographic information system (GIS) integrates hardware, software, and data for capturing, managing, analyzing, and displaying all forms of geographically referenced information [41].

[2] A shapefile stores nontopological geometry and attribute information for the spatial features of a data set. The geometry for a feature is stored as a shape comprising a set of vector coordinates [41].

6.1 System design

A top level system design for simulating pest species population dynamics in sugarcane is proposed in this section. Although the focus in this dissertation is on *E. saccharina* population dynamics, a similar design may be utilised not only for simulating other pest species in sugarcane, but also in other agricultural crops. Many mathematical and simulation models in agriculture tend to be developed in isolation, only focussing on one part of the agricultural ecosystem. The challenge to integrate all these different models remains, i.e. to model the interaction between host plants, pest species and environmental dynamics more precisely.

The system proposed here consists of four interacting subsystems within a specified spatial domain, namely the *Pest species population dynamics*, the *Sugarcane dynamics*, the *Environmental dynamics* and the *Economics* subsystems, as illustrated in Figure 6.1. The interaction between the subsystems is illustrated by means of arrows. Sugarcane pests cause damage to the sugarcane plant which, in turn, influences the plant growth and the revenue that may eventually be generated during harvesting time. The environment, which may include temperature, rainfall and soil type, influences plant growth which, in turn, influences the food resource available to the pest species. It is illustrated (in simplified terms) how these different modules may be integrated into a system which simulates the agricultural ecosystem. More research is, however, required to thoroughly understand and model the interaction between these subsystems in a realistic manner, with the main challenge in modelling the interaction between the pest species and the host plant.

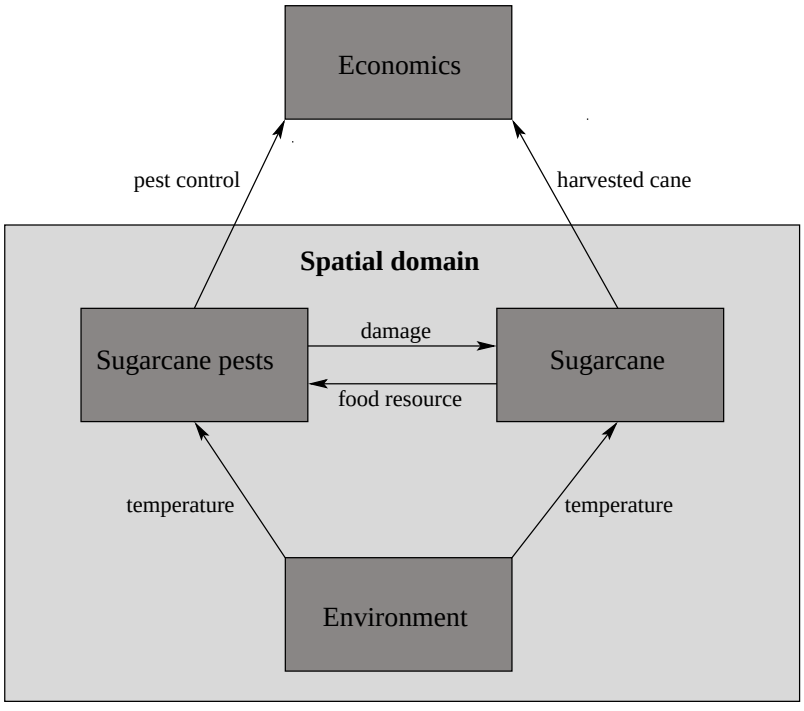


FIGURE 6.1: *The system designed for simulating pest species population dynamics in sugarcane.*

For the illustrative purposes of this study, the *Pest species population dynamics* subsystem includes only *E. saccharina* population dynamics (excluding all other pest species attacking sugarcane) under the influence of SIT (excluding all other control measures). The *Sugarcane dynamics* subsystem includes a simplified sugarcane growth and harvest model which has especially been developed for the purposes of this study. A number of more realistic mathematical

and simulation models have been developed in other studies for sugarcane growth and environmental dynamics [18, 94, 95]. When extending the simulation tool to a DSS, these models may be incorporated — along with models of other sugarcane pest species and their corresponding control measures — thereby forming a large integrated selection of models developed for use in the sugarcane industry. The different subsystems are described in more detail in the sections that follow.

6.1.1 The spatial domain

The spatial domain on which the different subsystems are modelled, describes the layout of the sugarcane area. The layout includes the position, size, shape, age and variety of the different fields contained within the sugarcane area, as well as the paths between the fields. The spatial domain may either be a real sugarcane domain obtained by means of imported GIS shapefiles (i.e. an irregular domain), or a simulated domain (with rectangular fields) entered via the graphical user interface.

Irregular domains

An algorithm for importing GIS shapefiles as matrix data structures (developed by Potgieter [83]), was implemented in MATLAB [102] using its MAPPING TOOLBOX [103]. A discretization of the domain is achieved by imposing a rectangular grid topology with grid points of intersection 5 m apart over the domain — resulting in a 25 m^2 patch size[3]. In order to perform simulations on the discretized domain, the rectangular grid topology is transformed to a matrix structure containing the entries '0', '1' and '2' in order to distinguish between patches inside a field, edge patches and non-sugarcane patches, respectively (see Figure 6.2). The following assumptions are made:

1. *Closed domain.* All spatial domains are assumed to be closed domains with zero-flux Neumann boundaries, therefore no dispersal of moths across the boundary is allowed (from outside or from inside the domain).

2. *Paths.* The paths separating the fields from each other are either ignored, or in areas where the fields are more than 30 metres[4] apart, are considered to be boundaries across which no dispersal of moths may occur between fields at these points.

3. *Edge patches.* An edge patch is defined as a patch which contains the boundary line of a certain field (see Figure 6.2). A section of each edge patch may contain non-sugarcane areas (for example a section of a separating path) — these areas are assumed to contain sugarcane, and therefore being part of the nearest field. The total area of the implemented domain is therefore slightly larger than the actual size of the domain. If an edge patch is shared between two different fields, the patch is assigned to only one of the fields.

4. *Heterogeneity.* The different fields in the domain are assumed to be heterogeneous in terms of crop age and variety, in accordance with the information contained in the GIS shapefiles.

[3] A patch size of 25 m^2 is considered appropriate, representing a habitat size within which the mean-field assumption is realistic. This patch size may, however, be changed in the model implementation if necessary.

[4] A distance of 30 metres seems appropriate according to numerical results obtained in Chapter 5. This distance may, however, be changed in the model implementation if necessary.

5. *Boundary conditions.* The boundary conditions of §5.3.1 are assumed, with boundaries occurring along the edges of the fields nearest to the surrounding non-sugarcane areas. In cases where fields are too far apart, these isolated fields are considered separate spatial domains with no dispersal of moths occurring between different spatial domains.

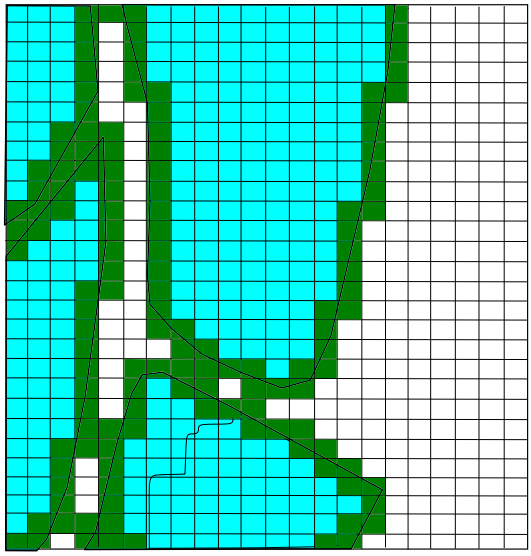
a)  b) 

FIGURE 6.2: *Discretization of the spatial domain. a) The pilot site field layout near Eston. b) The discretized domain corresponds to the red square in a) and was transformed to a matrix data structure in* MATLAB *containing the entries '0', '1' and '2' (represented by white, blue and green, respectively) denoting patches inside a field, edge patches and non-sugarcane patches, respectively.*

Rectangular domains

For domains containing fields of rectangular or square shape, not all of the assumptions for irregular domains are applicable. For example, no non-sugarcane areas exist within these domains. In order to distinguish between patches inside a field and edge patches, a matrix data structure is formed containing the entries '1' and '2' representing within-field and edge patches, respectively (see Figure 6.3). The following assumptions are made:

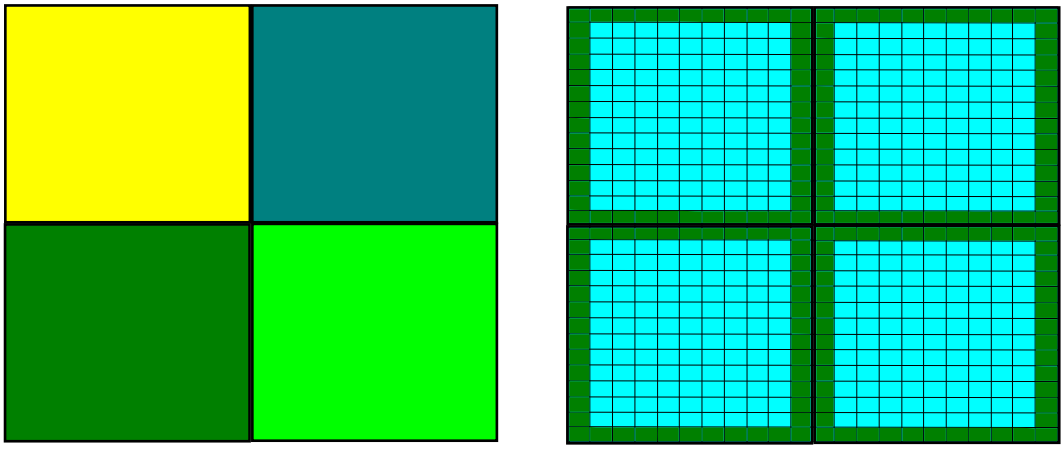
1. *Closed domain.* All spatial domains are assumed to be closed domains with zero-flux Neumann boundaries, therefore no dispersal of moths across the boundary is allowed (from outside or from inside the domain).

2. *Paths.* The paths separating the fields from each other are ignored and not included in the domain setup.

3. *Edge patches.* An edge patch is defined as a patch which contains the boundary line of a certain field (see Figure 6.3).

4. *Heterogeneity.* The different fields in the domain are assumed to be heterogeneous in terms of crop age and variety, in accordance with the input specified.

5. *Boundary conditions.* The boundary conditions of §5.3.1 are assumed, with boundaries occurring along the edges of the simulated domain.



a) b)

FIGURE 6.3: *a) Discretization of a rectangular spatial domain containing four different crop ages (represented by different colours). b) The discretized domain is transformed to a matrix data structure in* MATLAB *containing the entries '1' and '2' (represented by blue and green, respectively) denoting patches inside a field and edge patches, respectively.*

The graphical user interface provides a means of simulating rectangular domains containing fields of different sizes, ages and varieties, and arranged according to specified patterns. The patterns implemented include fields distributed in lanes and in a checkerboard formation, as illustrated in Figure 6.8.

6.1.2 The pest species subsystem

The main focus in this dissertation is on the development of appropriate mathematical models for *E. saccharina* population dynamics under the influence of SIT. The pest species subsystem therefore includes only *E. saccharina* population dynamics. Mathematical models similar to the ones described in Chapters 4 and 5 may, however, be developed for other important pest species in sugarcane. The most important pest species in South African sugarcane include stalk borers (of which *E. saccharina* is the most significant), soil pests (which include white grubs[5] and nematodes[6]), and leaf feeders (which include different species of grasshoppers and thrips[7]). Mathematical models describing the population dynamics of the above-mentioned pest species (under the influence of certain control measures) may all be integrated in the pest species subsystem as illustrated in Figure 6.4. The interaction between the different species (i.e. the effect that one species may have on the population growth of another species), however, still needs to be understood more thoroughly before realistic attempts at integrating the different models are possible. Environmental factors and the food resources from the host plant influences the population growth of the different species. The different species feed on different parts of the sugarcane plant, and therefore the sugarcane growth model will have to include information on

[5]Sugarcane in South Africa is attacked by various scarabaeid beetles (Coleoptera: Scarabeidae). The larvae of these insects are generally referred to as white grubs. Larvae feed on and damage roots of the sugarcane plant, thereby reducing growth and crop yield [113].

[6]Many species of plant-parasitic nematodes feed on the roots of sugarcane. These microscopic worm-like animals may cause serious damage to the roots of sugarcane, thereby reducing crop yield as well as the number of high yielding ratoons.

[7]Thrips are tiny, slender insects with fringed wings which feed on a large variety of sources, including sugarcane, by puncturing the source and sucking up the contents. In the right conditions, many species can exponentially increase in population size and form large swarms.

roots, stalks and leaves. The total damage caused to the sugarcane plant may be described by means of a crop damage index, which may then be used in the *Sugarcane growth* subsystem to translate the amount of damage to the percentage of sucrose lost. The total amount of control applied to the different pest species may be used by the *Economics* subsystem to estimate the cost of the control measure.

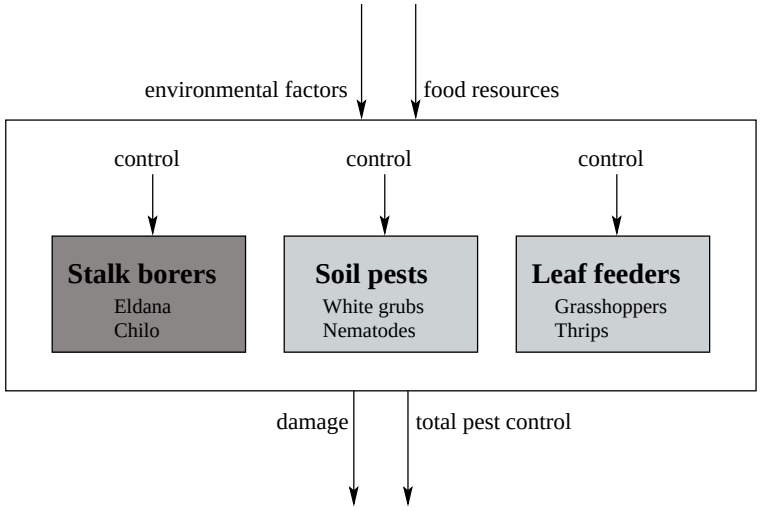


FIGURE 6.4: *The pest species subsystem which may include all the important pest species in South African sugarcane. The total damage caused by the different pest species may be estimated by such a system. In this dissertation, only the E. saccharina module is developed.*

The *E. saccharina* module developed for the purposes of this dissertation as part of the pest species subsystem utilises the spatio-temporal model described in Chapter 5, and includes the dynamics of all *E. saccharina* life stages under the influence of the control measure SIT, as illustrated in Figure 6.5. This module may be extended to include other control measures, such as biological control and habitat management. The following assumptions are made with respect to *E. saccharina* infestation and dispersal:

1. *Initial infestation.* The initial larval infestation levels of newly planted or harvested fields are assumed to be between 0 and 1 e/100s [35]. The percentage of blocks infested in the discretized domain at age 0 may range from 0% to 100%. Assuming the value of 100% means that *E. saccharina* infestation is uniformly distributed across a field. Assuming infestation occurring in less than 100% of the field causes the specified percentage of blocks to be selected randomly according to a uniform distribution. For older cane fields, the initial infestation levels at the start of the simulations are estimated by means of the mean-field model described in Chapter 4. Initial values of fertile egg, larval, pupal and moth population densities are computed according to the relations described in §5.3.2.

2. *Growth.* Growth, maturation and mortality parameters are employed as described in §4.4.

3. *Dispersal.* Dispersal is assumed to occur only from edge patch to edge patch between two fields. Realistic domains, such as those resulting from uploading GIS shapefiles, may contain non-sugarcane patches. Dispersal only occurs from edge patch to edge patch in these domains provided that the edge patches are not more than 30 m apart[8]. Longer

[8] A small portion of moths have been recorded to disperse up to 200 m during their lifespan, which is equivalent to an average of between 30 and 40 m per day [25].

range dispersals across fragmented landscapes are not explicitly considered in this dissertation. When assuming a small percentage of randomly selected within-field blocks to contain infestation, however, the situation may resemble infestation caused by longer range dispersal in contrast to infestation caused purely by diffusion from neighbouring fields.

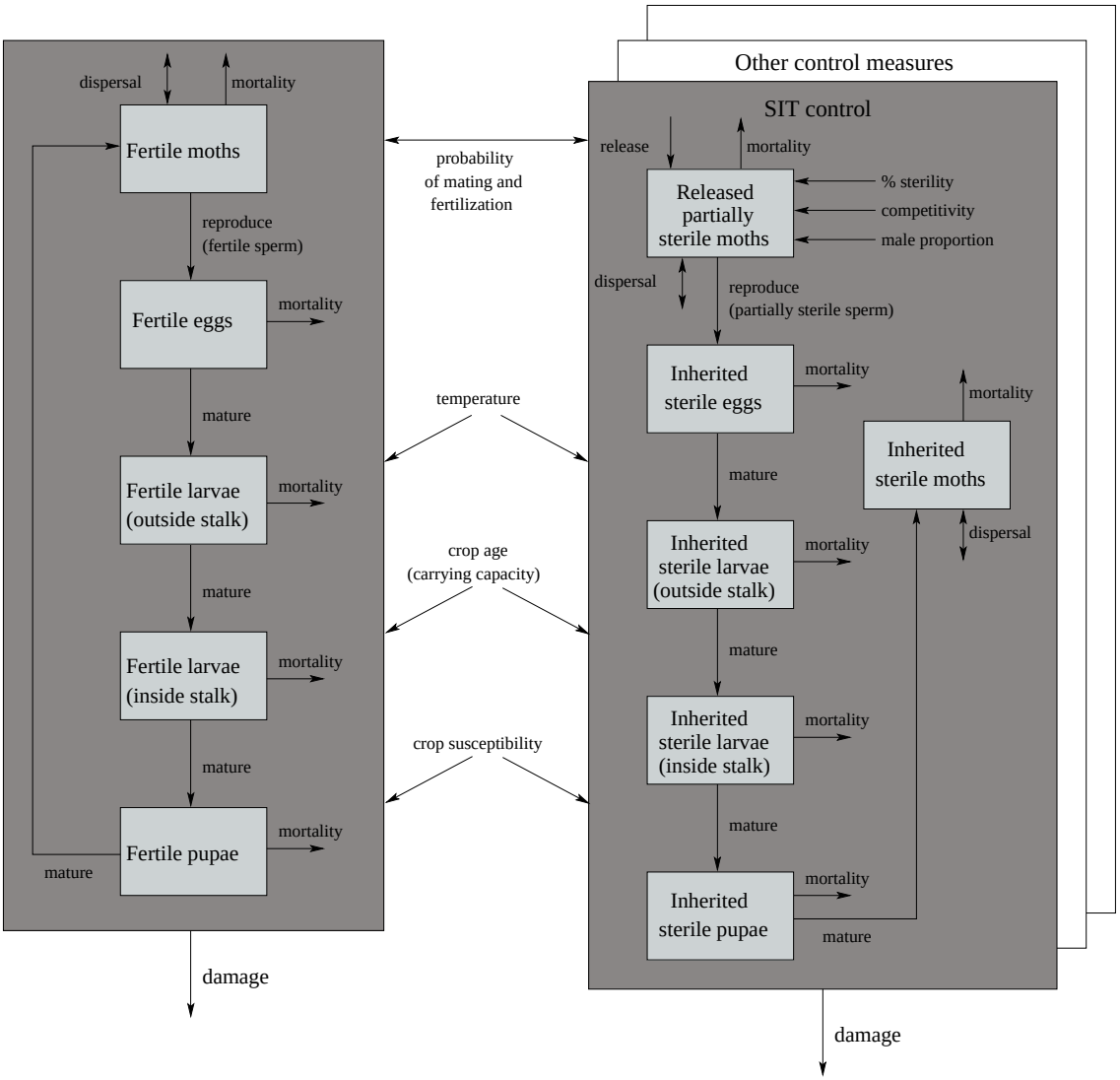


FIGURE 6.5: *The E. saccharina module developed in this study. The module describes the dynamics of all E. saccharina life stages under the influence of SIT. Other control measures may also be included, but are not considered explicitly in this study.*

Sterile insect releases by means of aircraft or ATVs driven alongside the edges of sugarcane fields may be simulated in the domain, with releases performed daily, twice a week, weekly or two-weekly. Once a field is harvested, SIT commences again after the crop reaches a certain minimum age. The following assumptions are made:

1. *ATV releases.* The released moths are assumed to spread uniformly along the edge patches of each field (or grouping of fields) where SIT is applied, with the edge patches of older fields requiring larger numbers of released moths than newly planted fields. In terms of irregular domains, one of the shortcomings of the finite-difference method is that it does

not accommodate complicated geometries very effectively — this issue is highlighted by the manner in which edge patches are defined and how releases occur in these patches. When edge patches form a straight line in relation to the grid topology, releases occur in one row or column of patches, whereas if releases occur diagonally in relation to the grid topology, more edge patches (and therefore more release sites) occur than in a horizontal or vertical line (see Figure 6.2).

2. *Distance travelled.* The paths surrounding the sugarcane fields should all be visited at least once during each SIT release. The distance travelled on the release site is approximated by the sum total of the perimeters of the fields (or groupings of fields) where sterile releases occur. A better approximation may, however, be obtained[9] by defining the distance travelled as a Chinese postman problem (CPP)[10] and employing suitable CPP algorithms to solve for the shortest possible circuit.

6.1.3 The sugarcane subsystem

The sugarcane subsystem includes a simplified model of sugarcane dynamics, illustrated in Figure 6.6. Sugarcane growth is influenced by a number of environmental factors, including temperature, rainfall and the type of soil [18]. The damage caused by different sugarcane pest species also has an impact on sugarcane growth. In this dissertation, however, only temperature and damage caused by *E. saccharina* are included as variables in the sugarcane model. The model developed in this dissertation estimates the stalk length as a function of time and temperature, and sucrose percentage as a function of damage caused by *E. saccharina* boring. Interaction between *E. saccharina* population growth and sugarcane growth is described by means of (4.38) — the older the cane, the higher the carrying capacity (more food resources) and corresponding infestation and damage levels.

The stalk length is estimated by the function (4.41), which was obtained from the CANEGRO model [18, 55], with temperature as the only independent variable. Ideal growing conditions are assumed. The function (4.41) may need to be adjusted to suit lower rainfall areas, such as in (4.50), for example. No explicit temporal models for sucrose (S), fibre (F) and non-fibre (N) content in cane were included in the model formulation — these values are instead estimated at harvest time only, using data from previous seasons. The function (4.44) for estimating sucrose percentage at harvest time was formulated in this dissertation using data from a previous study conducted on sugarcane growth and yield at Gingindlovu, KwaZulu-Natal [44]. In (4.44), the sucrose and stalk mass are both influenced by the percentage internodes damaged — no other environmental factors were included in the formulation as variables for estimating sucrose percentage. Incorporating output from the CANEGRO model [55] and CaneSim model [94, 95] may be a valuable addition. The values for F and N are, however, not estimated by CANEGRO [18, 100] or any explicit function, but rather taken as industry averages for a specific year. Refining the revenue estimation may include site-specific estimation of F and N by means of regression analysis, as described in the study by Stray [100], rather than assuming industry averages.

No distinction in cane growth is made between a newly planted crop and ratoon crops. The harvesting of cane is included in the subsystem, albeit in very simplified terms — fields are

[9] The release workers may not necessarily travel along an optimal route.

[10] In graph theory, the CPP is modelled by an undirected weighted graph whose edges represent the paths to be travelled, and whose vertices represent the intersections between the paths, with weights assigned to the edges to reflect the relevant distances. The objective is to find a shortest possible circuit that visits every edge at least once [119].

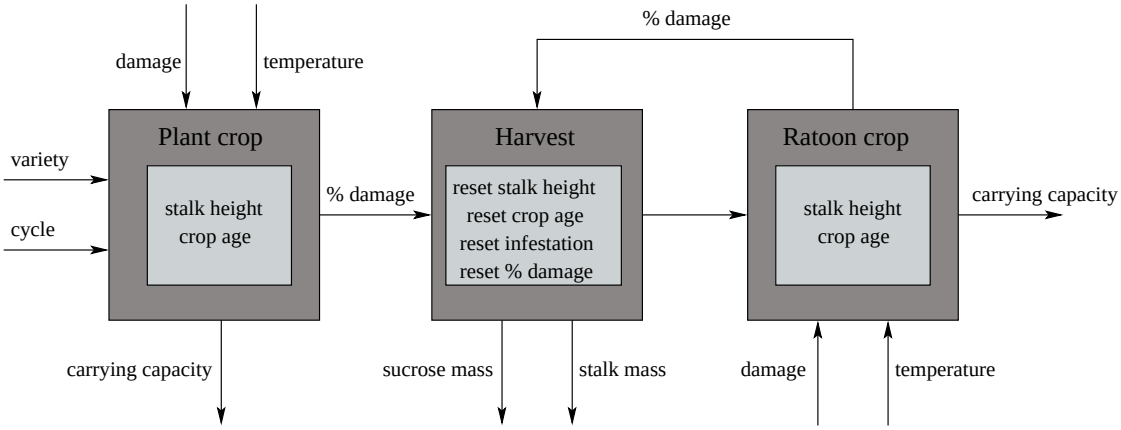


FIGURE 6.6: *A model representing sugarcane dynamics as implemented in the simulation tool.*

assumed to be harvested at the end of a sugarcane cycle, namely either at 12 or 24 months, with harvesting assumed possible during any month of the year. The closed-mill period between November and April is therefore not taken into consideration, nor are the *E. saccharina* infestation levels — a farmer would typically harvest a field when infestation and damage reach a certain level, which may be as early as 14–16 months. Once a field is harvested, revenue is generated using the estimated values for S, F and N and a new cycle is assumed to start immediately, with initial infestation as described in §7.3.2. A more realistic approach may include harvesting only during the period April to November when the mills are open, and also to include a carry-over decision for cane maturing during the closed-mill period. The decision may be based on expected damage levels when mills re-open, as described in the study by Horton [52]. A further refinement may include harvest scheduling algorithms, as considered in the study by Stray [100].

6.1.4 The environment subsystem

The only environmental factor considered as an independent variable in the models formulated in this dissertation, is temperature. No mathematical model for daily temperature estimation was, however, included. Monthly average temperatures were used instead. Incorporating models for environmental factors such as soil type, rainfall and temperature prediction may be a valuable addition to the system.

6.1.5 The economics subsystem

Investigating the economic viability of a pest control measure is important from a farm owner's perspective. A pest control measure (or combination of control measures) is considered economically viable if the increase in revenue as a result of implementing the measure is greater than the cost involved in implementing the measure. The economics module developed in this study includes the estimation of the RV percentage, expected revenue and the cost of control. No other farm expenditures were taken into account, and as such only the profit or loss[11] expected from applying pest control measures is estimated. The RV percentage is calculated by means of (4.43). The corresponding revenue is then estimated using (4.45), with the increase in revenue

[11]The profit or loss is defined as the increase in revenue expected less the cost of applying a pest control measure.

estimated by means of (4.46). The profit or loss to the farmer, as a result of applying a specific control measure or combination of control measures, is estimated using (4.47)

The manner in which edge patches are defined for irregular domains, with non-sugarcane areas potentially forming part of an edge patch, originally resulted in the total revenue for the domain being slightly overestimated. A better approximation was subsequently obtained by adjusting the total revenue according to the proportion of the original domain in relation to the implemented domain.

6.2 Simulation implementation

The computerised platform or simulation tool is a collection of MATLAB scripts with a corresponding graphical user interface. As such, an installation of MATLAB is required on a personal computer in order for the tool to function. In order to simulate an *E. saccharina* infestation scenario, Algorithm 6.1 was implemented in MATLAB. The algorithm combines calculations from the four different subsystems described in the previous section, performed for a specified domain in order to calculate the final estimated SIT profit, infestation level and crop damage index. The input required includes a discretization of the domain $\mathcal{S}$, the layout of the sugarcane fields contained in $\mathcal{S}$ with information regarding their initial crop ages, crop resistance ratings, field perimeters and field areas. The initial stalk length and density-dependent mortality rate at the start of the simulation is then calculated accordingly. All *E. saccharina* growth and dispersal parameters are also required, as well as SIT specific parameters (as described in §4.4).

6.2.1 Initialisation

At the start of the algorithm, the initial *E. saccharina* infestation on the domain is determined by utilising the mean-field model of Chapter 4 to find appropriate infestation levels for different crop ages. The mortality and maturation polynomials are also determined at the start of the algorithm (see §4.4.3 and §4.4.5).

6.2.2 The main loop

The algorithm first performs calculations assuming no SIT releases, after which the release ratio η (as specified in the input), is used in calculations. During each time step, the temperature is determined for the specific day. The mortality and maturation rates are then determined accordingly using the mortality and maturation polynomials. The stalk length bored at temperature τ is also determined using the reciprocal of the maturation rate multiplied by 42.525 (see §4.5.3).

The algorithm then continues by determining the set of positions in the discretized domain which are considered candidate sugarcane patches for SIT releases. In order to be a candidate site for SIT, the crop age at a position must fall within a minimum and maximum crop age range specified as input. Also, depending on the release method, SIT is only applied along the predetermined release lanes in the domain. After the candidate positions have been determined, the release rate at each position is determined according to the chosen release ratio and the infestation level at the start of SIT releases. The release cost is also calculated in a manner similar to the method explained in §5.12.

Algorithm 6.1: Algorithm for estimating the SIT profit.

Input : An $m \times n$ matrix $\mathcal{S}^{(d)}$ representing the discretisation of the domain $\mathcal{S}$. The sugarcane parameters, initial crop age (a), stalk length ℓ and crop resistance (ω) for each position in $\mathcal{S}^{(d)}$. The parameters y and z in the density-dependent function b. The *E. saccharina* maturation, mortality, diffusion and growth parameters (α, μ, d and λ_f). The SIT parameters release ratio (η), release frequency (θ), release method, cost per sterile (κ_r), labour cost per hectare (κ_l), fuel cost per hectare (κ_f), residual fertility (q), fertile fraction in F_1 generation (β), competitivity coefficients (c_m, c_s, c_f), sterile male proportion (m) and the number of matings per female and male (A and B). The day in the year on which the simulation is started (startTime) and the total number of simulated days (duration).

Output: *E. saccharina* infestation for all life stages and the crop damage index in all $(i,j) \in \mathcal{S}^{(d)}$, and the percentage profit estimated as a result of SIT ($P_{\%}$).

$\underline{\mathcal{E}}(\underline{x}, startTime) \leftarrow \underline{e}(\underline{x}, a)$ (Initialise infestation at initial crop age a across the domain)
determine mortality and maturation polynomials ($k(\tau)$ and $g(\tau)$)
for *zero and positive release ratio* η **do**
  while *startTime* $< t <$ *(startTime + duration)* **do**
    determine temperature τ on day t
    determine $\mu(t,\tau)$ and $\alpha(t,\tau)$ for all life stages
    determine stalk length bored per larvae $\sigma(t,\tau)$
    determine the set of positions $\mathcal{S}_t^S \subseteq \mathcal{S}^{(d)}$ in which SIT is applied
    if $\mathcal{S}_t^S \neq \emptyset$ **then**
      foreach $(i,j) \in \mathcal{S}_t^S$ **do**
        determine release rate $r(i,j,t)$
      calculate release cost $c(t)$
    foreach $(i,j) \in \mathcal{S}^{(d)}$ **do**
      calculate crop damage index $\delta(i,j,t)$
      calculate density-dependent mortality $b(i,j,t)$
      calculate probabilities of mating $P_{ff}(i,j,t)$, $P_{im}(i,j,t)$ and $P_{rm}(i,j,t)$
      calculate probabilities of fertilization $\gamma(i,j,t)$ and $\rho(i,j,t)$
      calculate the diffusion term $\nabla \cdot [\mathbf{D}(i,j)\nabla \underline{\mathcal{E}}(i,j,t)]$
      calculate the reaction term $\underline{f}(i,j,t)$
      $\underline{\mathcal{E}}(i,j,t+1) \leftarrow \underline{f}(i,j,t) + \nabla \cdot [\mathbf{D}(i,j)\nabla \underline{\mathcal{E}}(i,j,t)]$ (update infestation level)
      $\ell(i,j,t+1) \leftarrow \ell(t) + 0.16(24)(-1.32 + 0.176(\tau - 10))$ (update stalk length)
      $a(i,j,t+1) \leftarrow a(i,j,t) + 1$ (update crop age)
    determine the set of positions $\mathcal{S}_t^H \subseteq \mathcal{S}^{(d)}$ to be harvested
    foreach $(i,j) \in \mathcal{S}_t^H$ **do**
      calculate percentage sucrose S
      calculate revenue $W(i,j,t)$
      $\ell(i,j,t) \leftarrow 0$ (reset stalk length)
      $a(i,j,t) \leftarrow 0$ (reset crop age)
      $\underline{\mathcal{E}}(i,j,t) \leftarrow \underline{e}(i,j,0)$ (reset infestation)
      $\delta(i,j,t) \leftarrow 0$ (reset crop damage index)
  $C \leftarrow \sum c(t)$ (calculate total SIT cost)
  $W \leftarrow \sum W(i,j,t)$ (calculate total revenue)
$P_{\%} \leftarrow \frac{100(W_{SIT} - W - C)}{W}$
return $P_{\%}$, $\underline{\mathcal{E}}$ *and* δ

The algorithm then loops through all positions in the discretized domain and calculates the crop damage index using (5.13), the density-dependent mortality according to (4.38), the probabilities of mating by means of (4.26), (4.27) and (4.28), and the fertilization probabilities by means of (4.37). The dispersal rate (diffusion term) and population growth (reaction term) at each position is determined according to (5.7). The population size for the next time step is then calculated, as well as the stalk length and crop age.

Before continuing to the next time step, all the positions in the discretized domain that are ready for harvesting, are determined. For all positions which may be harvested, the final sucrose value at harvest time is calculated using (5.15), along with the estimated revenue according to (5.16). The stalk length, crop age and crop damage index are reset to zero, and the *E. saccharina* infestation level is reset to an initial infestation level assumed at age zero.

6.2.3 Termination

After the last time step, the total SIT cost is calculated for all positions, as well as the total revenue estimated for the entire domain. The percentage SIT profit is determined after the algorithm has looped through both a scenario without SIT and a scenario with SIT. The percentage SIT profit, *E. saccharina* infestation level and percentage damage are returned as output.

6.3 The graphical user interface

The appearance and functionality of the SIT simulation tool graphical user interface are described and illustrated in this section. The correct procedures to follow at each step when simulating a specific scenario are described in this section and Appendix A. Upon execution of the simulation tool, the graphical user interface, shown in the screenshot in Figure 6.7 appears[12]. For each scenario, a simulation start time and end time should be chosen. The output produced at the end of the simulation will be valid for the chosen period.

The *Simulation start time* and the *Simulation end time* input fields contain two drop-down menus each, one indicating the month, and the other indicating the year at which the simulation is started.

The graphical user interface also contains two panels, each with specific input fields that have to be populated by the user in order to finally run a simulation and obtain output for a specific scenario. The relevant procedures to follow within the graphical user interface's respective panels are described in the sections that follow.

6.3.1 The sugarcane input parameters

The input parameters required for creating an appropriate sugarcane domain on which an *E. saccharina* infestation may be simulated, are listed below.

Sugarcane cycle This input field contains a drop-down menu from which the user may either select '1 year' or '2 year', corresponding to the sugarcane cycle in the region for which the simulation is run. Harvesting of fields occur at a crop age of 12 months for a one-year cycle and at 24 months for a two-year cycle.

[12]The matlab code for the graphical user interface was written by JJ Potgieter [83].

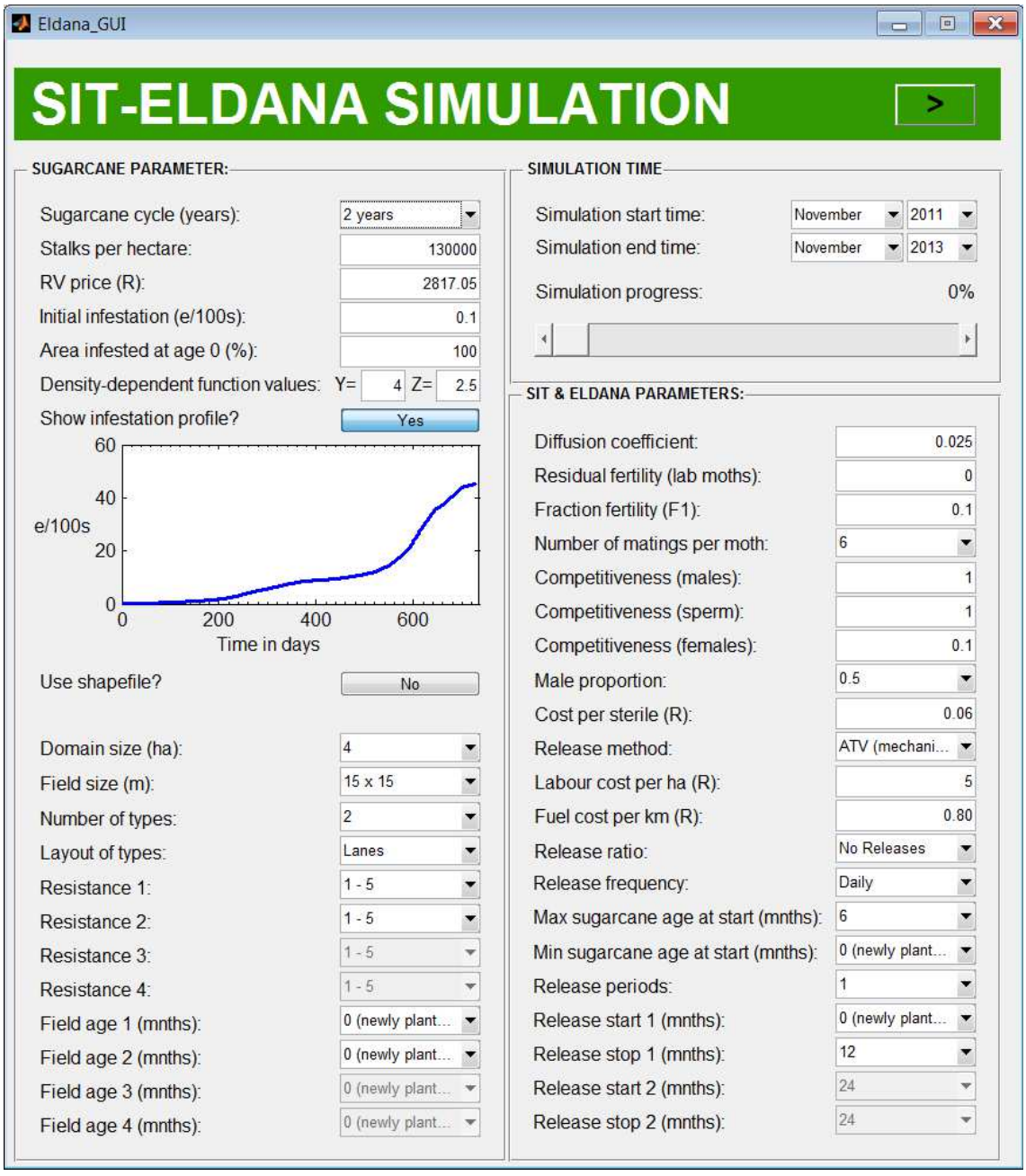


FIGURE 6.7: *The graphical user interface designed for the SIT simulation tool.*

Stalks per hectare This heading contains a numeric input field in which the user may enter a value corresponding to the number of stalks per hectare expected in the region for which the simulation is run. The default value is 130 000.

RV price (R) This heading contains a numeric input field in which the user may enter a value, specified in South African Rands, which corresponds to the appropriate average RV price for the chosen simulation period. The default value is R2 817.05.

Initial infestation (e/100s) This heading contains a numeric input field in which the user may enter a value reflecting the average level of infestation, specified as e/100s, occurring

in some or all areas of a field after harvest time or in a newly planted field. The default value is 0.1.

Area infested at age 0 (%) This heading contains a numeric input field in which the user may enter a value between 0 and 100 reflecting the percentage of area in a harvested or newly planted field which contains the levels of initial infestation entered under *Initial infestation (e/100s)*.

Density-dependent function values This heading contains numeric input fields y and z in which the user may enter values for the parameters y and z of the density-dependent mortality function (4.38). These values determine the shape of the infestation profile. The default values are 4 and 2.5, respectively.

Show infestation profile This heading contains a toggle button with the options 'Yes' and 'No'. Selecting 'Yes' produces a graph illustrating the expected infestation over time (infestation profile). The graph is produced by using the mean-field model, described in Chapter 4, for a field starting from age 0 until the end of the sugarcane cycle period, and should correspond to the typical infestation experienced in the region for which the simulation is run.

Use shapefile? This heading contains a toggle button with the options 'Yes' and 'No'. Selecting 'Yes' allows the user to specify a .shp file from a chosen location on the computer as input. The data required for input, which should be contained in the uploaded shapefile, include field perimeter, area, age, and variety. Upon selecting 'No', the user is prompted to populate the input fields *Farm size*, *Field size*, *Variation*, *Number of types*, *Layout of types*, *Resistance 1*, *Resistance 2*, *Resistance 3*, *Resistance 4*, *Plant date 1*, *Plant date 2*, *Plant date 3* and *Plant date 4*.

Domain size (ha) This input field contains a drop-down menu from which the user may select '1 hectare' , '2 hectare' or '4 hectare'. All areas within the simulated domain are assumed to contain sugarcane. The default value is '4 hectare'.

Field size (m) This input field contains a conditional drop-down menu depending on the *Domain size* selected. For a '1 hectare' domain, the options '15 × 15 m', '15 × 100 m', '20 × 20 m', '20 × 100 m', '25 × 25 m', '25 × 100 m', '30 × 30 m', '30 × 100 m', '35 × 35 m', '35 × 100 m', '40 × 40 m', '40 × 100 m', '45 × 45 m', '45 × 100 m', '50 × 50 m', '50 × 100 m' and '100 × 100 m' are available for selection. For a '2 hectare' domain, the options are identical, with the added option of '100 × 200 m' available for selection. For a '4 hectare' domain, the options are identical to the '2 hectare' domain, with the added option of '200 × 200 m' available for selection. The fields are assumed to be separated by paths, which are utilised to perform SIT releases by means of ATVs.

Number of types This input field contains a drop-down menu from which the user may select '1', '2' , '3' or '4'. The subsets in the domain are populated with n crop ages according to the number of types selected. However, the number of crop ages in a domain also depend on the number of subsets within the domain. A domain containing only two subsets, for example, will have at most two crop ages present in the domain.

Layout of types This input field contains a drop-down menu from which the user may select 'Lanes', 'Checkerboard', 'Tablecloth' or 'Random'. These layouts correspond to the layouts illustrated in Figure 6.8.

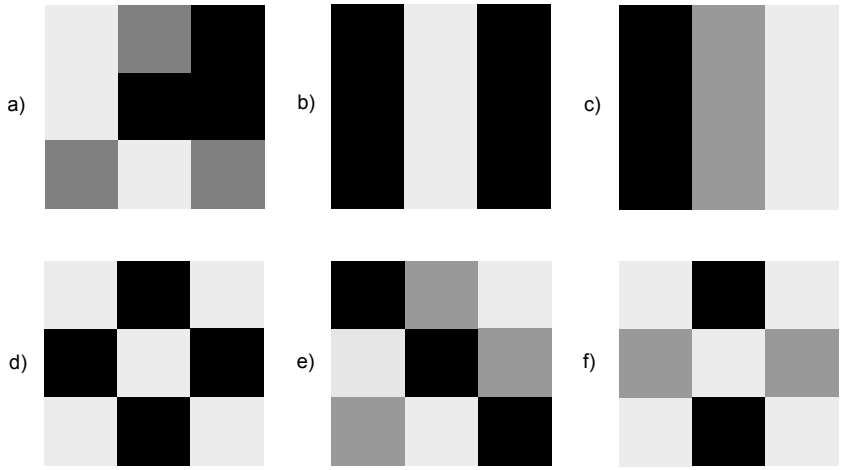


FIGURE 6.8: *Spatial patterns formed by differently aged subsets (each crop age is represented by a unique colour) in the domain. a) A random pattern, b) two age categories distributed in lanes, c) three age categories distributed in lanes, d) two age categories distributed in a checkerboard pattern, e) three age categories distributed along diagonals in a checkerboard pattern, f) three age categories distributed in an alternative checkerboard pattern. The patterns, as well as the dimensions, of the subsets are varied in simulations.*

Resistance rating 1 This input field contains a drop-down menu from which the user may select '1–5', '6', '7', '8', '9' or '10'. The value selected should correspond with the resistance rating of the sugarcane variety in the specific subset. The default value is '1–5'.

Resistance rating 2 input field contains a drop-down menu identical to the *Resistance rating 1* input field. The input field is enabled when selecting '2', '3' or '4' in the *Number of types* input field. The default value is '1–5'.

Resistance rating 3 This input field contains a drop-down menu identical to the *Resistance rating 1* input field. The input field is enabled when selecting '3' or '4' in the *Number of types* input field. The default value is '1–5'.

Resistance rating 4 This input field contains a drop-down menu identical to the *Resistance rating 1* input field. The input field is enabled when selecting '4' in the *Number of types* input field. The default value is '1–5'.

Field age 1 (mnths) This input field contains a conditional drop-down menu from which the user may select 'Newly planted', '1 month', '2 month', '3 month', etc. If the sugarcane cycle is 1 year, the drop-down menu has options up to '12 month', if the sugarcane cycle is 2 years, the drop-down menu has options up to '24 month'. The values chosen should correspond to a crop age contained within a certain grouping of the subsets.

Field age 2 (mnths) This input field is identical to the *Field age 1 (mnths)* input field. This input field is enabled if the *Number of types* is greater than 1.

Field age 3 (mnths) This input field is identical to the *Field age 1 (mnths)* input field. This input field is only activated if the *Number of types* is greater than 2.

Field age 4 (mnths) This input field is identical to the *Field age 1 (mnths)* input field. This input field is only activated if the *Number of types* is greater than 3.

6.3.2 The SIT and Eldana input parameters

The required input parameters which are related to *E. saccharina* growth and dispersal and the application of SIT are listed below.

Diffusion coefficient This heading contains a numerical input field in which the user may enter a value between 0.005 and 0.03, corresponding to the range given in §5.4.1. The default value is 0.025. The diffusion coefficient reflects how fast *E. saccharina* moths disperse across the domain.

Residual fertility (lab moths) This heading contains a numerical input field in which the user may enter a value between 0 and 1. The residual fertility corresponds to the fraction of released moths which are still fertile due to inefficient radiation. The default value is 0.

Fraction fertility (F1) This heading contains a numerical input field in which the user may enter a value between 0 and 1. The fraction fertility indicates the fraction of the F1 generation that does not inherit an assumed 100% sterility, but are fertile, as described in §4.4.7. The default value is 0.1. F2 inherited sterility is not taken into account in this dissertation, and the F1 generation is assumed to be either 100% sterile, or 100% fertile.

Number of matings per moth This input field contains a drop-down menu from which the user may select '1', '2', '3', '4', '5' or '6'. The value selected should correspond to the maximum number of matings possible per *E. saccharina* moth in sugarcane as described in §4.4.1. The default value is '6'.

Competitiveness (males) This heading contains a numerical input field in which the user may enter a value between 0 and 1. The value entered should indicate the expected competitiveness of a released semi-sterile male compared to a wild male as a fraction, as described in §4.4.6. The default value is 1.

Competitiveness (sperm) This heading contains a numerical input field in which the user may enter a value between 0 and 1. The value entered should indicate the expected competitiveness of sperm from released semi-sterile males compared to sperm from wild males as a fraction, as described in §4.4.6. The default value is 1.

Competitiveness (females) This heading contains a numerical input field in which the user may enter a value between 0 and 1. The value entered should indicate the expected competitiveness of released sterile females compared to wild females as a fraction, as described in §4.4.6. The default value is 0.1.

Male proportion This input field contains a drop-down menu from which the user may select '0', '0.5' or '1'. The value selected should correspond to the proportion of males to females in SIT releases. The default value is 0.5.

Cost per sterile (R) This heading contains a numerical input field in which the user may enter a value specified in South African Rands. The value entered should reflect the cost of rearing and sterilising one *E. saccharina* moth, excluding the labour and fuel cost incurred as a result of sterile releases. The default value is 0.06.

Release method This input field contains a drop-down menu from which the user may select 'ATV (mechanical)' or 'Aerial'. The default value is 'ATV (mechanical)'. The option selected determines the method of distribution of sterile releases. For releases by means of ATVs, SIT releases will occur alongside release lanes (the edges of the fields) in both a simulated domain and a domain specified by uploading a GIS shapefile. If releases are by means of aircraft, release flight paths are assumed to be 100 m apart, with the distribution of sterile moths as a Gaussian distribution along the release paths.

Labour cost per ha (R) This heading contains a numerical input field in which the user may enter a value specified in South African Rands. The value entered should reflect the labour cost per hectare for releasing sterile moths. The default value is 5.00.

Fuel cost per km (R) This heading contains a numerical input field in which the user may enter a value specified in South Africa Rands. The value entered should reflect the fuel cost per km for releasing sterile moths. The default value is 0.80.

Release ratio This input field contains a drop-down menu from which the user may select 'No releases', '1:1', '2:1', '3:1', '4:1', '5:1', ... , '40:1'. The option selected indicates the ratio of sterile moths released to the total number of *E. saccharina* moths present in a certain field at the commencement date of SIT application. All the sterile moths are released uniformly along the release lanes or paths.

Release frequency This input field contains a drop-down menu from which the user may select 'Daily', 'Twice a week', 'Weekly' or 'Bi-weekly'. The option selected indicates the frequency with which SIT application occurs in the domain.

Max sugarcane age at start (mnths) This input field contains a drop-down menu from which the user may select 'Newly planted', '1 month', '2 month', '3 month', ... , '24 month'. The option chosen determines which fields are candidates for SIT application at the start of the simulation. The default value is '12 month'.

Min sugarcane age at start (mnths) This input field contains a drop-down menu from which the user may select 'Newly planted', '1 month', '2 month', '3 month', ... , '24 month'. The option chosen determines which fields are candidates for SIT application at the start and during the simulation. Fields that are at least as old as the minimum sugarcane age at the start and during the simulation, will have SIT applied. Furthermore, once a field is harvested, it has to reach the minimum crop age before SIT application commences again. The default value is '6 month'.

Release periods This input field contains a drop-down menu from which the user may select '1' or '2'. If '2' is selected, *Release start 2* and *Release stop 2* are activated. The release periods determine the crop age period within a sugarcane cycle at which SIT will be applied to a specific field.

Release start 1 This input field contains a drop-down menu from which the user may select 'Newly planted', '1 month', '2 month', '3 month', ... , '12 month' or '24 month', depending on the *Sugarcane cycle* chosen. The option chosen indicates the crop age at which SIT should commence within each field. The default value is '6 month', and should be greater than or equal to the *Min sugarcane age (at start of release)*.

Release stop 1 This input field contains a drop-down menu from which the user may select 'Newly planted', '1 month', '2 month', '3 month', ... , '12 month' or '24 month', depending on the *Sugarcane cycle* chosen. The option chosen indicates the crop age at which SIT application is terminated within a certain field. The default value is '24 month', and should be greater than or equal to *Release start 1*.

Release start 2 This input field contains a drop-down menu from which the user may select 'Newly planted', '1 month', '2 month', '3 month', ... , '12 month' or '24 month', depending on the *Sugarcane cycle* chosen. If a second release period occurs, the option chosen indicates the crop age at which SIT commences again after the first release period. The option chosen should be larger than the option chosen for *Release stop 1*.

Release stop 2 This input field contains a drop-down menu from which the user may select 'Newly planted', '1 month', '2 month', '3 month', ... , '12 month' or '24 month', depending on the *Sugarcane cycle* chosen. If a second release period occurs, the option chosen indicates the crop age at which SIT is terminated during the second release period. The option chosen should be larger than the option chosen for *Release start 2*.

6.3.3 The output values

Once the user has specified input values in all the aforementioned input fields, the simulation may be started by clicking on the start button in the top right corner (see Figure 6.7). When the simulation starts, a progress bar indicates how far the simulation is from completion. While the simulation is running, a 3D-illustration of infestation across the domain during each time step appears. The following output graphs are available for further analysis at the end of the simulation:

- Average infestation across the domain as a function of time,
- Average larval infestation per field at harvest time,
- Average % damage per field at harvest time,
- Average revenue per hectare per field at harvest time,
- Average *E. saccharina* larval infestation per field at the end of the simulation,
- A 2D-illustration of % damage across the domain at the harvest time of each field, and
- A 2D-illustration of infestation across the domain at the end of the simulation.

6.4 A realistic application scenario

The pilot site near Eston, Kwazulu-Natal, with field layout as shown in Figure 6.9, was chosen to illustrate the working of the simulation tool described in the previous sections. This site was chosen due to its isolation and the fact that it is surrounded by other land uses, which correspond to the model assumptions made (a closed domain with zero-flux Neumann boundaries). The site comprises a total of 45 hectares of sugarcane varieties N12, N37, N31, N44, N45 and N50, all of which have resistance ratings to *E. saccharina* of either 4 or 5. The sugarcane field layout is heterogeneous in terms of crop age and, for the purposes of the simulations performed, were assumed similar to data obtained in 2009 [54]. In these data, the age of the sugarcane varied from 1 to 17 months (see Figure 6.9), with a sugarcane growth cycle of 24 months. Furthermore, infestation levels of fields aged between 14 and 17 months were on average below 10 e/100s (see Table 6.1), although some of the fields reached levels of 21 e/100s at an age of 14 months.

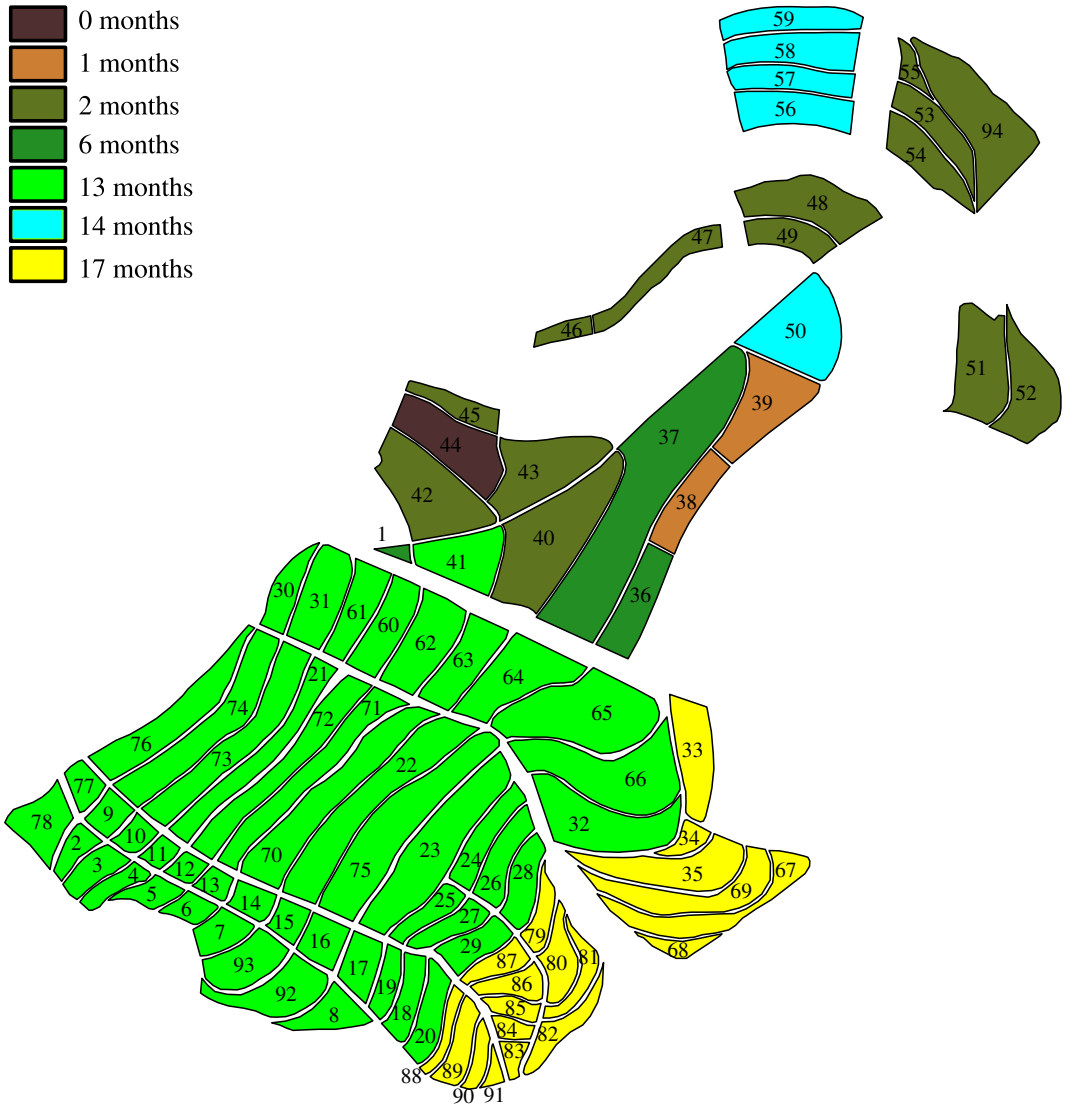


FIGURE 6.9: *The sugarcane field layout of the SIT pilot site near Eston [54]. Labels assigned to the fields of the pilot site are as contained in the shapefiles.*

Month	Crop age (months)	e/100s	% Stalks red
Jul / Aug	14	7.14	6.75
Aug / Sept	15	5.73	8.59
Sept / Oct	16	3	6.77
Oct	17	6.8	5.12

TABLE 6.1: *Summary of data obtained for the period July to October 2009 at the pilot site.*

6.4.1 The input values

The initial crop ages contained in the shapefiles were rounded to the nearest month. The number of stalks per hectare was assumed to be 130 000 and the RV price was taken as R2817.05. An *E. saccharina* infestation of 0.1 e/100s was assumed within 100% of the area in each field (i.e. uniformly distributed within each field). No fields were therefore excluded from infestation. The following assumptions were made with respect to *E. saccharina* population growth and dispersal:

Growth Growth, maturation and mortality parameters were assumed as described in §4.4. The number of matings per moth were assumed to be 6. The density-dependent mortality function had to be adjusted according to previous infestation data. However, not enough data for the pilot site were available in order to estimate suitable values for y and z. A density-dependent mortality function

$$b(t) = \frac{4}{(d^{2.5} + 1)}$$

was therefore assumed, which corresponds to the density-dependent function assumed in the simulations performed in §5.7.

Dispersal Dispersal was assumed to occur at a constant rate of 0.025 per 25 m^2 per day.

Sterile insect releases by means of ATVs driven alongside the edges of the sugarcane fields were simulated, with releases performed once a week. Based on the results of the sensitivity analyses in §4.9, fields were considered possible release sites only if the cane age was at most 6 months. Fields older than 6 months were initially excluded from sterile releases until harvested, with releases commencing during the following sugarcane cycle. The following assumptions were made:

SIT parameters The fertile proportion of the F_1 generation of released sterile males was set equal to 0.1, the residual fertility in released moths was taken as 0, the male and female competitiveness were set at 1 and 0.1, respectively, sperm competitiveness was taken as 1, and sterile releases included both males and females. For illustrative purposes the release ratios for all the fields in the domain were assumed to be 40 : 1 — the ratio adopted by Entomon Technologies (Pty) Ltd for sterile codling moth releases in orchards.

Release method ATV releases performed weekly with a mechanical device were assumed, since, for the above-mentioned release method, suppression may be achieved at smaller release ratios and larger distances between release lanes. The field layout renders suppression via manual ATV releases impossible in certain areas within the domain where

fields have a width of more than 35 m (according to numerical results presented in §5.7). Released moths were assumed to spread uniformly across the edge patches of each field, with the edge patches of older fields requiring larger numbers of released moths than newly planted fields.

Release cost The cost per sterile insect (excluding labour and fuel costs) was assumed to be R0.03, the labour cost per hectare was assumed R5 per application, and the fuel cost was taken as R0.023 per 100 m.

Release periods One release period was assumed, with releases commencing at age 0 and continuing up to harvest time.

6.4.2 Numerical results

At time $t = 0$, when the simulation was started, heterogeneous cane ages of 0, 1, 2, 6, 13, 14 and 17 months across the fields were assumed. Harvesting occurred at times $t = 215$, $t = 305$, $t = 336$, $t = 550$, $t = 670$, $t = 701$ and $t = 731$ for fields aged 17, 14 ,13, 6, 2, 1 and 0 months, respectively. Weekly sterile releases commenced at time $t = 0$ only in fields of age at most 6 months. For fields older than 6 months, sterile releases commenced after harvesting. At time $t = 336$, all the fields aged 13 months were harvested, resulting in a sudden decrease in average infestation levels over the entire domain. For $t > 336$, sterile moths were released across the entire domain. At a release ratio of 40 : 1 in each respective field, sterile releases resulted in suppressed average *E. saccharina* infestation levels (below 5 e/100s) over the domain (see Figure 6.10).

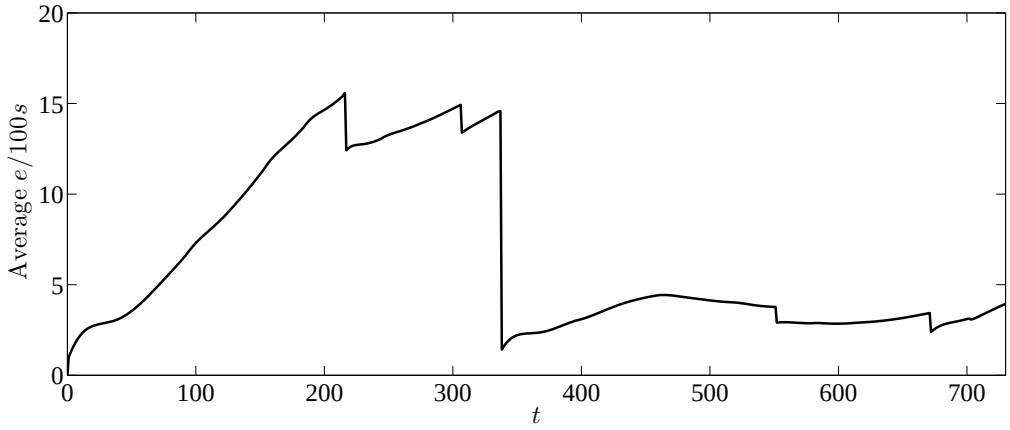


FIGURE 6.10: *Average larval infestation simulated for the pilot site near Eston with weekly sterile releases commencing only in fields of age at most 6 months.*

Closer examination of the simulation results revealed that, although the average infestation levels for the entire domain were suppressed below 5 e/100s, some fields did not experience suppression — release lanes were too far apart, resulting in higher infestation levels in the middle of the corresponding fields where sterile moth population densities were too low. Figure 6.11 shows average larval infestation levels per field at harvest time — sterile releases were performed only in fields 1, 36–40, 42–49, 51–55 and 94 before the respective harvest times during the 24 month simulation period. Suppression in fields 1, 36, 38, 45–47, 49, 53–55 was

easily achieved — release ratios less than 40 : 1 may also have been effective in these fields, thereby reducing the release cost. Suppression below 5 $e/100s$ was, however, not achieved in fields 37, 39, 40–44, 48, 51, 52 and 94. Release lanes around these fields were too far apart in order to achieve suppression in the middle of these fields, corresponding with the results obtained for weekly releases in §5.7. Figure 6.12 contains a spatial overview of the percentage damage at each field's respective harvest time.

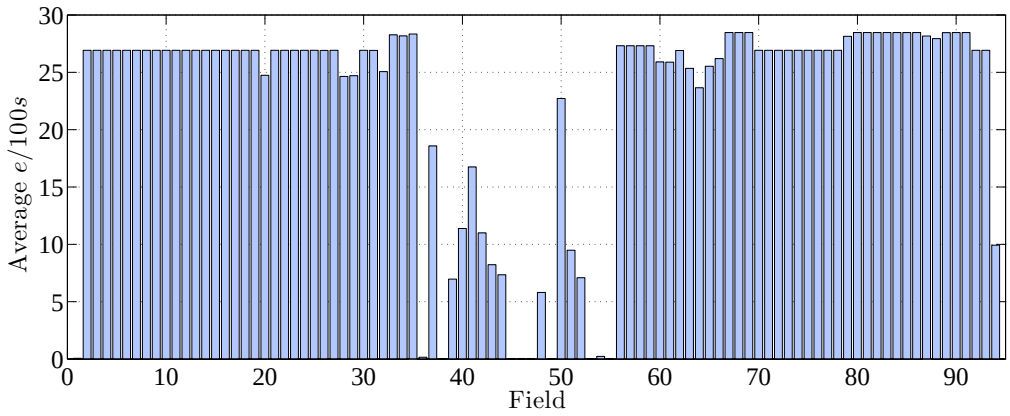


FIGURE 6.11: *Average larval infestation per field at harvest time for the pilot site near Eston. Weekly sterile releases commenced only in fields of age at most 6 months.*

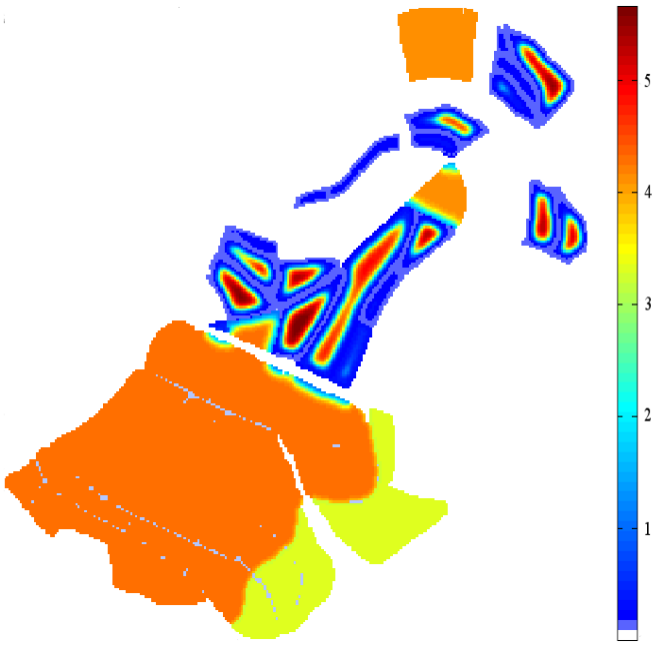


FIGURE 6.12: *A spatial overview of the percentage damage per field at harvest time for the pilot site near Eston.*

From Figures 6.11 and 6.12, it may be verified that field 41, a 13 month-old field at time $t = 0$ and surrounded by 2 month-old fields, experienced decreased infestation levels compared to the other 13 month-old fields as a result of sterile releases occurring in the neighbouring fields. This is also evident to a lesser extent in fields 20, 28, 29, 32, 60, 61 and 63–66 which are adjacent

to fields in which sterile releases occurred prior to the harvesting of fields 20, 28, 29, 32, 60, 61 and 63–66. Fields 33–35, 79, 87 and 88, which were 17 month-old fields at time $t = 0$ and adjacent to 13 month-old fields, experienced slightly reduced infestation levels compared to the other 17 month-old fields as a result of dispersal to the neighbouring fields where infestations levels were lower. Figure 6.13 shows the average percentage damage per field at harvest time, and corresponds with the infestation levels per field shown in Figure 6.11. However, the 17

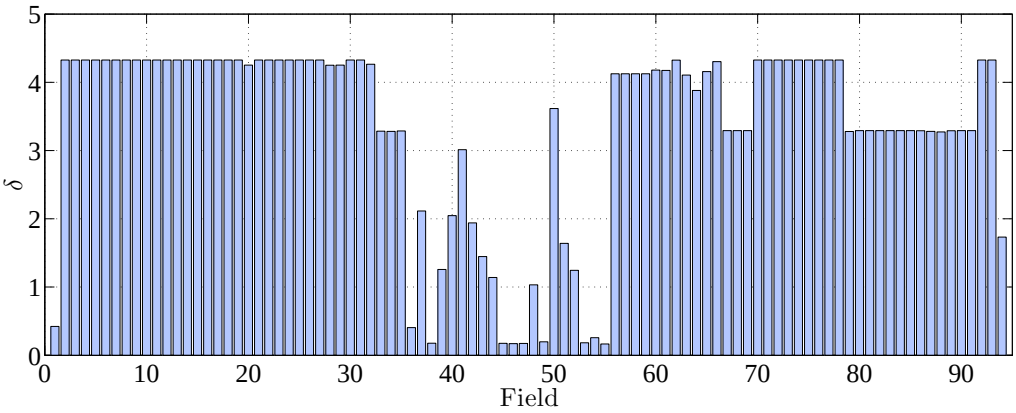


FIGURE 6.13: *Average percentage damage per field at harvest time for the pilot site near Eston.*

month-old fields experienced slightly less damage than the 13 and 14 month-old fields — this may be due to the different months during which the cane was planted. The average revenue realised per 25 m^2 in each field at harvest time are shown in Figure 6.14. All the fields in which SIT was applied before harvesting (even the fields in which suppression was not obtained) show a clear increase in revenue as a result of decreased infestation levels. Fields 20, 28, 29, 32, 41, 60, 61 and 63–66, which are adjacent to fields in which sterile releases occurred prior to the harvesting of the first mentioned fields, also show slightly increased revenue compared to that of the other fields which are of similar age. Figure 6.15 shows average larval infestation levels per field at time $t = 731$, whereas Figure 6.16 presents a spatial overview of larval infestation levels per field in the spatial domain at time $t = 731$ — sterile releases were performed across the entire domain by the end of the simulation, with fields aged 0, 1 and 2 months at the start of simulation harvested just before the end of the simulation — therefore the suppression effect of released sterile moths is not yet evident in Figures 6.15 and 6.16. It was concluded that, from the results obtained at harvesting of each field and the results obtained at the end of the simulation, suppression below 5 e/100s was not achieved in fields 23, 31, 32, 37, 39, 40–44, 48, 50–52, 62, 64–66, 75, 78 and 92–94.

The total revenue for the domain over the 24 month simulation period was approximately R1 160 000, which translates to a loss in revenue of approximately 5%. A simulation without sterile releases was also performed in order to obtain the approximated SIT profit for the 24 month simulation period considered. The total revenue for the domain over the 24 month period without sterile releases was approximately R1 025 000, which translates to a loss in revenue of 16%. The percentage increase in revenue for the period as a result of SIT is therefore 13%. The total cost of applying SIT over the 24 month simulation period, at a release ratio of 40 : 1 in all the fields, was approximately R270 700, or approximately 200% of the increase in revenue as a result of SIT. Compared to the SIT cost, the first two years of applying SIT appeared not to be economically viable. However, in the year following the simulated 24 month period, the 13–17 month-old fields (with sterile releases performed since the last harvest time) would have been harvested, resulting in a further increase in revenue. From Figure 4.6 the estimated revenue

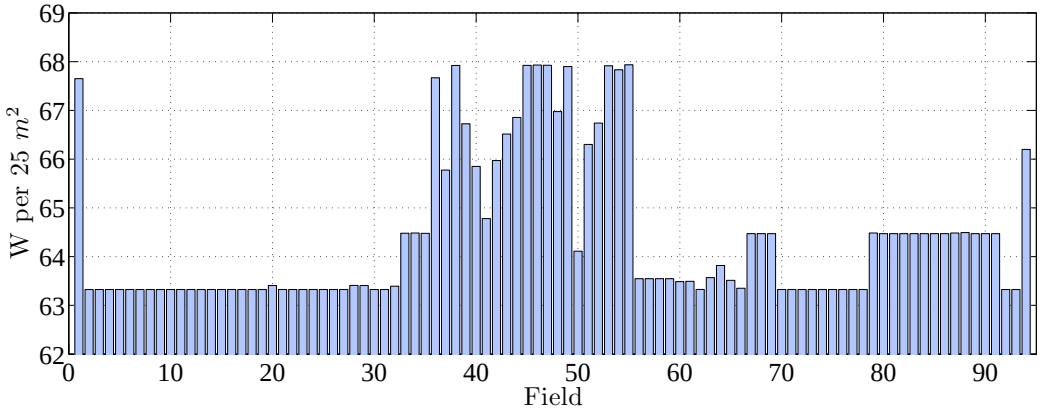


FIGURE 6.14: *Average revenue per 25 m^2 per field at harvest time for the pilot site near Eston.*

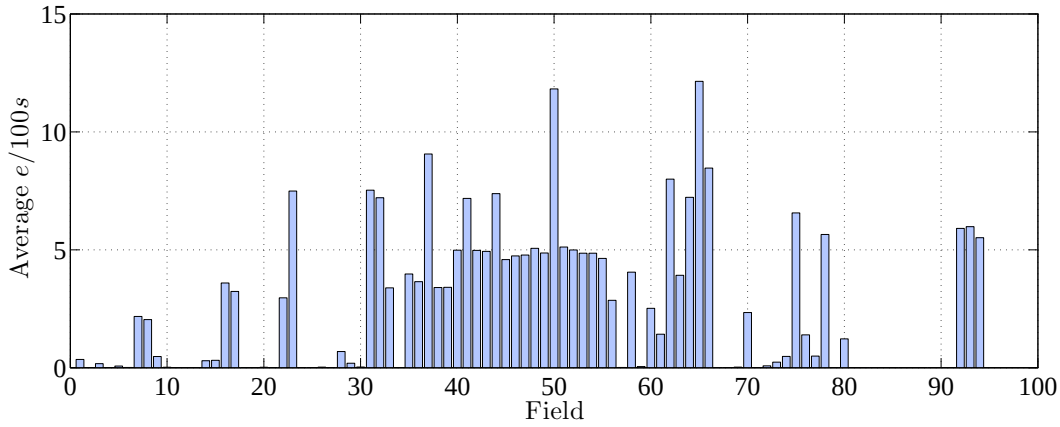


FIGURE 6.15: *Average larval infestation per field at the end of a 24 month simulated for the pilot site near Eston.*

for a 45 hectare domain where no *E. saccharina* damage occurs, is approximately R1 226 000, yielding a possible maximum increase in revenue of approximately 16%. In order to break even with the cost of applying SIT, the maximum increase should be at least 26% (200% of 13%). For the assumed release ratio, field layout and parameters, it appears that applying SIT by means of ATVs driven alongside the edges, and commencing SIT at age 0 to harvesting, is not an economically viable strategy.

6.4.3 Recommendations

In order to decrease the costs involved in applying SIT, the homogenous release ratio of 40 : 1 across the domain may be adjusted per field according to each field's size. Smaller release ratios are required for smaller areas. Suppression was not achieved in the fields where release lanes were too far apart. In order to achieve suppression, the following measures are proposed:

1. *Adjust the field layout.* The field layout may be adjusted such that the release lanes are not more than 35 metres apart (according to results obtained in §5.7). This will, in turn, reduce the release ratios required for suppression, thereby reducing the SIT cost.

FIGURE 6.16: *A spatial overview of larval infestation at the end of a 24 month simulation for the pilot site near Eston. The fields aged 0, 1 and 2 months were harvested just before the end of the simulation; therefore infestation levels are still low.*

2. *Release by foot.* Moths may be released by foot inside the fields where suppression is difficult to achieve when releases are only along the edges. However, this will be much more labour-intensive than releasing only by ATVs, and as a result may increase the application cost of SIT.

3. *Aerial releases.* Aerial releases may be more effective in the sugarcane context since then release distributions do not depend on field layouts. However, the current application cost involved in aerial releases causes the method not to be economically viable. If the application costs for UAVs are significantly lower, aerial releases may be considered as an economically viable release method.

Furthermore, SIT application was assumed on a weekly basis, commencing at age 0 and continuing for the entire 24 month period. There may be scope for adjusting the release period to a shorter time.

6.5 Chapter summary

This chapter contains a description of the SIT simulation tool developed by incorporating the spatio-temporal model of Chapter 5 so as to be applicable to various heterogeneous domains. A description of the system was given in §6.1, along with ideas for future expansion of the tool. In §6.3, a detailed description of the graphical user interface was provided. The input parameters required in order to perform simulations were specified, as well as the output values which are available at the end of a simulation. An example simulation was given as a proof of concept in §6.4, taking as the domain the pilot site near Eston, KwaZulu Natal. The results of the simulation were given in §6.4.2, with resulting recommendations given in §6.4.3. In order to

reduce the release cost, it was recommended that release ratios be adjusted per field according to each field's size, with smaller release ratios in smaller areas. Also, the release period may be shortened. Suppression was not achieved in fields which were too large — adjustment of the field layout was recommended such that release lanes are at most 35 metres apart. If the adjustment of the field layout is not feasible, aerial releases may be considered as a more effective release method in the sugarcane context.

CHAPTER 7

Diversification of sugarcane habitats

Contents

"Bring diversity back to agriculture. That's what made it work in the first place."

— David R. Brower

"I sometimes ponder on variation form and it seems to me it ought to be more restrained, purer."

— Johannes Brahms

In this chapter, modelling contributions are made towards the suppression of *E.saccharina* in different heterogeneous sugarcane layouts with respect to both sugarcane age and the harvesting of the sugarcane at different points in time. The reaction-diffusion model developed in Chapter 5 is utilised to perform simulations on a number of differently structured spatially heterogeneous domains.

7.1 Improving the cost-efficiency of SIT

As mentioned in Chapter 2, there has been a global shift towards improving the efficiency of pest control programs in such a way that they are long-term, environmentally friendly and cost-effective [20]. SIT has been recognised as a long-term and environmentally friendly solution, but arguments can be made against the cost-efficiency of SIT when compared to other successful control measures [48]. In contrast to a well known pest species such as tsetse (*Glossina pallidipes*

(Diptera: Glossinidae)), few alternative cost-efficient and long-term control measures exist for *E. saccharina*. Conventional control methods have been proposed and researched for the control of *E. saccharina* in sugarcane. Although contributing towards suppression, none of these have proven very successful in preventing *E. saccharina* infestations. Harvesting of sugarcane at a younger age is still considered the largest controlling factor of *E. saccharina* in sugarcane [7].

Results from Chapters 4 and 5 indicate that SIT may be a viable control measure if certain conditions are met. These include the dispersal capability of released sterile insects, method of release, distance between release lanes, frequency of releases, and the release ratio. In addition, results indicate that SIT may be an economically viable pest control method to use within the sugarcane industry if the cost per released sterile insect can be brought within a certain range. The cost of applying SIT, however, currently remains high and one possible way of reducing the cost-efficiency of SIT is further explored in this chapter.

The cost-efficiency of SIT may be improved significantly by reducing the cost per sterile *E. saccharina* (which includes rearing, labour and fuel costs) and/or by reducing the number of sterile insects required for suppression. The cost per sterile insect may be reduced once the SASRI rearing unit is at full production capacity (comparable with other rearing units) and with improved mass rearing technology. This rearing unit is, however, still in its research phase, with very limited production capacity. Further investigations into reducing the cost per sterile are not pursued in this chapter. The primary objective of this chapter is to investigate a means of reducing the field populations of *E. saccharina*, which will in turn reduce the number of sterile insects required for suppression without compromising the effectiveness of SIT — a true integrated pest management approach.

7.2 Infestation over heterogeneous domains

Resource availability for pest insects is often linked to changes occuring over the life cycle of the host plants. The plant growth stage is directly related to host suitability (quality of resources) and may, in turn, have an influence on infestation levels and movement patterns [69]. Infestation levels decrease to zero or almost zero in crop plants when harvested — immobile or semi-mobile life stages, such as *E. saccharina* pupae and larvae, are removed together with the harvested crop and mobile life stages, such as *E. saccharina* moths, are expected to adjust their foraging, mating and oviposition decisions to the local distribution and quality of resources. The manipulation of planting and harvesting schedules has been recognised to have a negative impact on pest populations [20]. This may be as a result of a more diverse habitat in terms of crop age. It has been shown that population densities of herbivore pest insects are often reduced in vegetationally more diverse habitats [69].

It may therefore be possible that suitably diversified sugarcane habitats (with respect to cane age) exist, where the harvesting of the different fields at different points in time have a negative impact on pest populations. Combining such field layouts with pest control methods may reduce the cost and effectiveness of achieving suppression. In the context of SIT, the number of sterile insects required for suppression may be less, which will improve the cost-efficiency of SIT.

7.3 Model implementation

Average infestation levels over time have been estimated by means of simulations of the finite-difference approximation (5.7), implemented in MATLAB on differently structured heterogeneous

spatial domains (in terms of crop ages), where harvesting occurs at different points in time for the differently aged crops in the domain. As before, sugarcane growing on a 24 month cycle (in the midlands north area of Kwazulu-Natal) was used as the standard for the simulations. Crop ages were grouped within certain categories in order to reduce the number of simulations required — either two cane age categories (0–12 months and 13–24 months), three cane age categories (0–8 months, 9–16 months and 17–24 months) or four cane age categories (0–6 months, 7–12 months, 13–18 months and 19–24 months). Homogenous domains were excluded from the simulations due to the risk of no diversification being too high — if anything happens, a farmer may loose his entire crop with no income in that particular sugarcane cycle. Only heterogeneous domains were therefore considered with at least two crop ages present in the domain (see Figure 6.8). The objective was to establish which field layout structure performs the best in terms of average infestation over time.

7.3.1 Spatial patterns considered

A rectangular spatial domain $\mathcal{S}$ was divided into smaller rectangular or square subsets $\mathcal{S}_i$ which are heterogeneous in terms of crop age. Mortality parameters are therefore heterogeneous across $\mathcal{S}$ — for differently aged crops, the larval mortality in each subset $\mathcal{S}_i$ was increased by a density-dependent mortality parameter, which is a function of crop age. Each subset $\mathcal{S}_i$ was further divided into a number of smaller rectangular or square fields, all with the same crop age (*ie.* homogenous patches were assumed within each subset $\mathcal{S}_i$). The different subsets were arranged according to the six spatial patterns shown in Figure 7.1. The average *E. saccharina* infestation levels over a set period of time were compared for these different patterns in order to establish for which field layout the average infestation level over time is minimised.

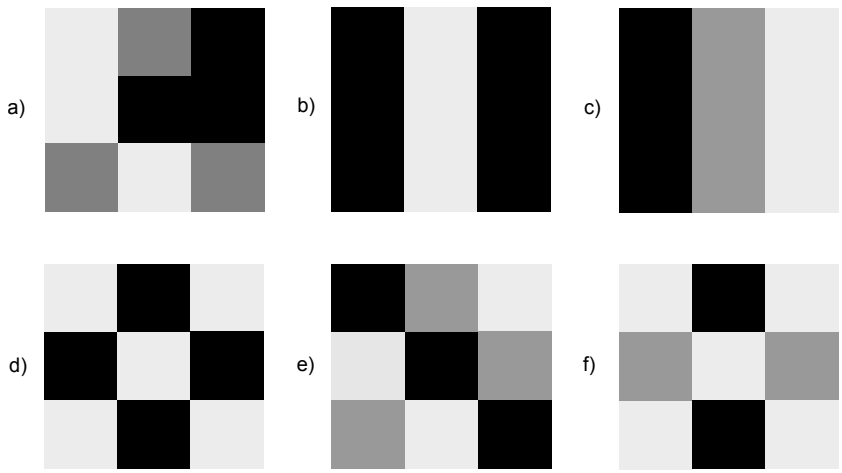


FIGURE 7.1: *Spatial patterns formed by differently aged subsets (each crop age is represented by a unique colour) in the domain. a) A random pattern, b) two age categories distributed in lanes, c) three age categories distributed in lanes, d) two age categories distributed in a checkerboard pattern, e) three age categories distributed along diagonals in a checkerboard pattern, f) three age categories distributed in an alternative checkerboard pattern. The patterns, as well as the dimensions, of the subsets are varied in simulations.*

7.3.2 Initial infestation levels

The simulation results of Chapter 5 are limited by the assumption that initial populations (at age 0) are distributed uniformly across the entire domain. The within-field distribution patterns of *E. saccharina* were found to be more clustered, with 'hot spots' occurring, rather than exhibiting an even spread across a field [16]. This uniformity assumption, however, remains a good approximation when modelling on a larger scale.

In a newly planted field, initial infestation may be zero or very close to zero in cases where *E. saccharina* eggs survived a previous harvest on the ground or in the seed stalk. After harvesting, initial infestation levels may in some cases be zero or very close to zero depending on how close the sugarcane is cut to ground level and how badly infested the field was at the time of harvest [35]. As a result of the more clustered within-field distribution which may have occurred in the field before the time of harvest, a small percentage of random 'hot spots' may still be infested with *E. saccharina* surviving close to the root stock and in the remaining parts of the stalks, or stubble.

Three possible initial infestations were therefore assumed in this chapter, namely 0% across the entire newly harvested/planted subset, low levels (0.1 e/100s) at a small percentage (1%) of randomly selected points (with 0 e/100s at all other points), and low levels uniformly spread across the entire (100%) of the harvested area. A newly planted field and a newly harvested field were assumed to have the same initial infestation.

Assuming that infestation occurs across 100% of the harvested area corresponds to the assumptions made in Chapter 5. Furthermore, no initial infestation (0%) after harvesting (*ie.* all *E. saccharina* life stages are removed during harvesting) corresponds to a scenario where infestation occurs in the form of diffusion from neighbouring infested areas (*E. saccharina* gradually spreading from the edges inwards). Finally, assuming infestation occurs only at randomly selected points in a newly planted/harvested area corresponds to a scenario where not all *E. saccharina* were removed at the time of harvest, where some of the seed cane were not clean, or where some moths do not only spread gradually, but are far flyers infesting neighbouring areas within-field and not only along the edges of fields.

7.3.3 Harvesting assumptions

The harvesting of sugarcane was assumed to occur at the end of the cycle of 12 or 24 months. Planting times were selected only between March and November so as to prevent harvesting occurring during the period between November and March when the mills are closed.

7.4 Simulation results

The diffusion coefficient, $d(\underline{x})$, was assumed to be constant at 0.025. Simulations were performed on a 4 hectare (200 m $\times$ 200 m) domain for a resistant sugarcane variety (with resistance rating smaller than 6) over a time period of 84 months. Initial infestation after harvesting was assumed to be either 0, or 0.1 $e/100s$ in 1% of the field area, or a homogenous initial infestation of 0.1 $e/100s$ across the entire field (100% of the field area). The density-dependent mortality function $b(t) = 4/(d^{2.5} + 1)$ was assumed. During each time step, the average of the infestation level across a heterogeneous domain was calculated from an infestation surface such as that in Figure 7.2. An example of the average infestation across the entire domain and computed over all time

steps is given in Figure 7.3. Different heterogeneous domains were compared using the average of the infestation level over time (the dotted line in Figure 7.3), denoted by E_{mean}, and the standard deviation from this average, denoted by E_{stdev}, as performance measures.

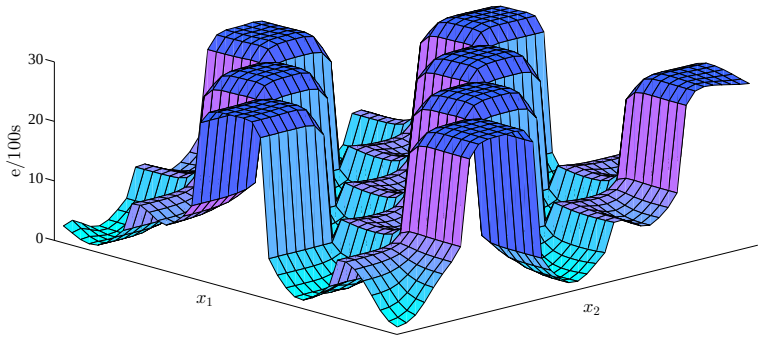


FIGURE 7.2: *Infestation level (e/100s) at a single time step across a 200 m × 200 m heterogeneous domain with three crop ages.*

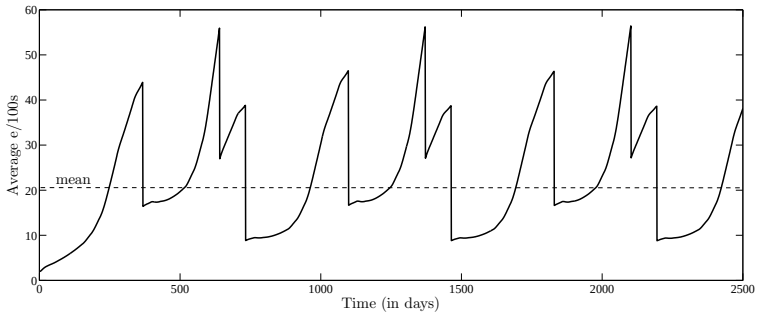


FIGURE 7.3: *The average infestation level (e/100s) over a heterogeneous domain with three crop ages, computed over a time period of 7 years.*

From Table 7.1, it is clear that E_{mean} is significantly lower over a heterogeneous domain, where subsets are larger (*e.g.* 100 m × 100 m), compared to smaller subsets (*e.g.* 40 m × 40 m). This difference is more apparent when assuming that initial infestation is mainly as a result of diffusion from neighbouring subsets (spreading from the edges inwards). At a 100% initial infestation (*ie.* homogenous initial infestation greater than zero across the entire subset), the differences in E_{mean} are insignificant. From Table 7.1, it may also be seen that E_{mean} is slightly lower over a heterogeneous domain with three crop ages than E_{mean} for a domain with only two crop ages present. This difference is not significantly influenced by the choice of initial infestation level. Furthermore, E_{mean} is lower over a heterogeneous domain with subsets of different crop ages arranged in lanes (according to the patterns b) or c) in Figure 6.8) compared to arranging subsets in a checkerboard pattern (according to the patterns d), e) or f) in Figure 6.8). Finally, domains where subsets form random spatial patterns yield a lower E_{mean} than when subsets are grouped according to a certain pattern.

Taking all of the above observations into account, it is clear that a domain where same-aged crops are grouped together (*ie.* n subsets for n crop ages) and with more than two crop ages

Pattern	Field dimension (in m)	Initial infestation 0% 2 ages	0% 3 ages	1% 2 ages	1% 3 ages	100% 2 ages	100% 3 ages
Checker 1	40×40	20.09	18.42	20.22	18.55	21.48	19.96
(Figure 6.8 (d,e))	100×100	12.19	11.71	15.68	14.58	21.37	20
Checker 2	40×40	N/A	18.76	N/A	18.92	N/A	20.31
(Figure 6.8 (f))	40×100	N/A	17.59	N/A	18.05	N/A	20.22
Lanes	40×200	18.09	17.04	19.79	17.45	21.17	20.06
(Figure 6.8 (b,c))	50×200	16.78	15.05	17.61	16.11	21.42	19.86
	100×200	8.04	N/A	14.25	N/A	21.34	N/A
Random	40×40	16.04	16.98		17.60		19.95
(Figure 6.8 (a))	100×100		8.35				

TABLE 7.1: *E_{mean} (e/100s) for the spatial patterns depicted in Figure 6.8, with no SIT applied. The crop ages were chosen such that, if only two ages were selected, the ages were 12 months apart for two-year cycle sugarcane, while if three ages were selected, the ages were 8 months apart.*

present, has a lower E_{mean} compared to domains where the opposite is true (same-aged crop separated and scattered across the domain according to some pattern). This is also reflected in random patterns performing better, since more same-aged crops are thus expected to be grouped together.

Dividing a domain into n subsets for n crop ages may be performed in a number of different ways. The problems of finding an optimal division of a domain, the division in terms of surface area occupied by the different crop ages, the choice of crop ages, and the order in which the crop ages are arranged next to one another, are considered in the following subsections.

7.4.1 Boundaries shared between subsets

A four-hectare domain (200 m × 200 m) divided into four subsets containing three ages according to a checker board pattern (100 m × 100 m blocks), and the same domain divided into lanes (50 × 200 m), as illustrated in Figure 7.4, have equal surface areas allocated to the different subsets for both patterns. The checker board pattern, however, yields a lower value of E_{mean}. This result is also observed when performing a simulation with four different crop ages arranged in similar patterns (see Figure 7.5). In both scenarios, the main difference is the length of boundaries shared between the different subsets. An optimal division of a certain domain into n different subsets containing n crop ages is one for which the expression

$$\sum_{i}^{n} f(\mathcal{S}_i) \tag{7.1}$$

is minimised, where the function $f(\mathcal{S}_i)$ denotes the total length of boundaries shared between subset $\mathcal{S}_i$ and other subsets. Minimising the total length of boundaries shared between subsets minimises the cross-infestation between different crop ages.

7.4.2 Surface area allocation of subsets

An optimal division of a domain into subsets does, however, not only depend on the expression in (7.1). For example, if a square domain is divided into four subsets containing four crop ages,

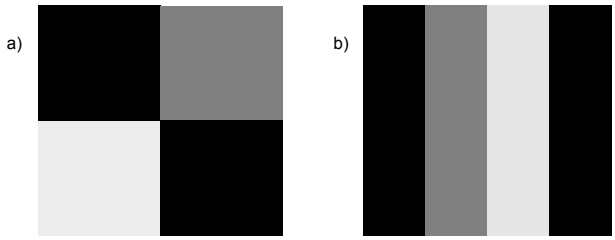


FIGURE 7.4: *A four-hectare (200 m × 200 m) domain divided into four subsets, with three crop ages present. a) E_{mean} = 11.71 e/100s if subsets are chosen as squares of dimensions 100 m × 100 m and assuming a 0% initial infestation after harvesting. b) E_{mean} = 15.05 e/100s if subsets are chosen as rectangles of dimensions 50 m × 200 m and assuming a 0% initial infestation after harvesting.*

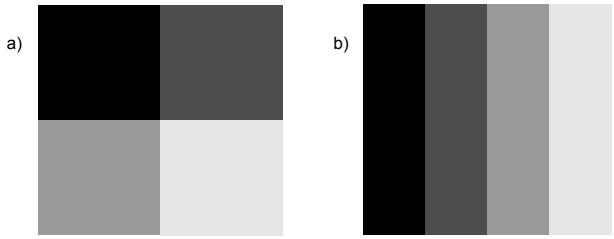


FIGURE 7.5: *A four-hectare (200 m × 200 m) domain divided into four subsets, with four crop ages present. a) E_{mean} = 11.64 e/100s if subsets are chosen as squares of dimensions 100 m × 100 m and assuming a 0% initial infestation after harvesting. b) E_{mean} = 15.66 e/100s if subsets are chosen as rectangles of dimensions 50 m × 200 m and assuming a 0% initial infestation after harvesting.*

the expression in (7.1) would be minimised for both a) and b) in Figure 7.7. Moreover, if a square domain is divided into two fields containing two crop ages, the expression in (7.1) is minimised for any division — one field may be very large and the other small. In order to establish whether the difference between the surface areas of different subsets should be minimised, a square four-hectare (200 m × 200 m) domain was divided into three subsets containing three crop ages, as illustrated in Figure 7.6, and also into four subsets containing four crop ages, as illustrated in Figure 7.7.

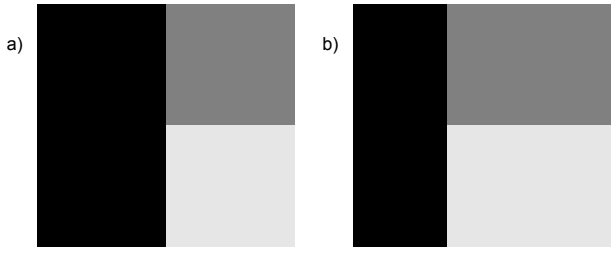


FIGURE 7.6: *A four-hectare (200 m × 200 m) domain divided into three subsets, with three crop ages present. a) The horisontal boundary between the subsets has length 100 m. b) The horisontal boundary between the subsets has length 133 m, thereby minimising the difference between surface areas of subsets.*

If a square domain is divided into three subsets containing three crop ages, the expression in (7.1) is minimised by dividing the domain as illustrated in Figure 7.6, but with two of the subsets as small as possible (*ie.* the length of the horisontal boundary between subsets in Figure 7.6 should be minimised). The difference between surface areas of different subsets becomes larger the smaller the expression in (7.1) is made. The value of E_{mean} is slightly less for a domain

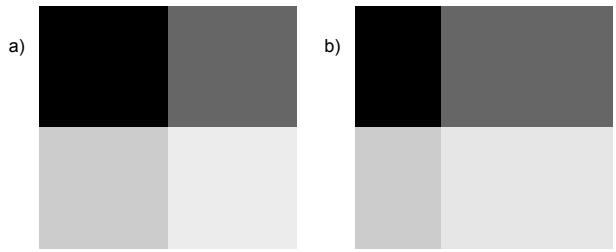


FIGURE 7.7: *A 4 hectare (200 × 200 m) domain divided into four subsets, with three crop ages present. a) Subsets are chosen as squares of dimensions 100 m × 100 m. b) Subsets chosen with unequal surface areas.*

where the expression in (7.1) is smaller (Figure 7.6 a)), but it does not differ significantly from simulations performed on a domain for which the difference between the surface areas of the subsets is minimised (Figure 7.6 b)). The standard deviation, E_{stdev}, on the other hand, is minimised if the difference between the surface areas of different subsets is minimised.

If a square domain is divided into four subsets containing four crop ages, the expression in (7.1) is minimised by dividing the domain as illustrated in both Figure 7.7 a) and b), with the difference in surface areas of the subsets additionally minimised in a). The value of E_{mean} does not differ significantly for the domains in a) and b). The standard deviation, E_{stdev}, on the other hand, is minimised if the difference between the surface areas of different subsets is minimised, which is consistent with the simulation results observed for three subsets containing three crop ages.

Although the difference in surface areas does not significantly influence the value of E_{mean}, it does significantly influence the value of E_{stdev} (see Table 7.2). A smaller standard deviation is considered better, since the height of the peaks (high infestation periods) in the average infestation across the domain will be smaller. Minimising the difference in surface areas of the various subsets is therefore considered better.

Number of crop ages	**Surface area**	**Initial infestation 0%** Average	Standard deviation	**1%** Average	Standard deviation	**100%** Average	Standard deviation
3 (Figure 7.6 (b))	equal	10.46	6.43	14.28	8.64	19.71	10.92
3 (Figure 7.6 (a))	unequal	10.15	7.24	13.77	8.84	19.98	11.31
4 (Figure 7.7 (a))	equal	11.64	6.61	14.67	8.14	20.06	10.65
4 (Figure 7.7 (b))	unequal	11.46	7.03	14.44	9.47	19.80	11.72

TABLE 7.2: *The values of E_{mean} and E_{stdev} for a domain divided into three or four subsets with equal or unequal surface area allocation to different crop ages.*

7.4.3 Variation in crop age

At 0% initial infestation after harvesting, a 200 m × 200 m domain containing only two crop ages, grouped into two subsets of equal surface area, yields a lower value for E_{mean} compared to a similar domain divided into three or more subsets containing three or more crop ages (see Table 7.3). This difference becomes insignificant if a small percentage of initial infestation is

allowed, and at 100% initial infestation, a domain containing more crop ages yields a slightly lower value of E_{mean}. An initial infestation greater than 0% is more likely to occur; a more diversified domain in terms of crop age is therefore considered to be better. The value of E_{stdev} is also minimised the more crop ages are present in a domain.

Number of crop ages	**Initial infestation** 0% Average	0% Standard deviation	1% Average	1% Standard deviation	100% Average	100% Standard deviation
2	8.04	7.83	14.25	12.95	21.34	16.3
3	10.46	6.43	14.28	8.64	19.71	10.92
4	11.64	6.61	14.67	8.14	20.06	10.65
6	14.42	6.86	16.07	7.77	19.95	9.62

TABLE 7.3: *The values of E_{mean} and E_{stdev} for a four-hectare domain divided into two, three, four or six subsets of equal area.*

A 200 m × 200 m domain containing four crop ages performs slightly worse in terms of average infestation levels compared to a domain containing three crop ages, but the corresponding value of E_{stdev} is slightly lower. A 200 m × 200 m domain containing six crop ages performs significantly worse in terms of average infestation levels compared to a domain containing two, three or four crop ages, but the corresponding value of E_{stdev} is significantly lower the larger the percentage of initial infestation becomes. This seems to contradict the observation that more diversification in terms of crop age is better. Closer examination of this phenomenon revealed, however, that the size of the domain influences the optimal number of crop ages. This is consistent with the results reported in Table 7.1, which indicate that larger subsets perform better than smaller subsets. A 200 m × 200 m domain is optimally divided into three subsets containing three crop ages. For a domain larger than four hectares, more than three crop ages may be optimal since the size of the subsets may be larger. Each differently sized and shaped domain, therefore, induces a different optimal division, depending both on the length of boundaries shared between the subsets and the surface areas allocated to the different subsets.

Subsets with different crop ages may be arranged differently within a certain domain. The three different ways in which four subsets containing different crop ages may be arranged in a square domain are illustrated in Figure 7.8. Simulations indicate that there is no significant difference in the resulting values for E_{mean} and E_{stdev} for the three different arrangements (see Table 7.4). However, minimising the age difference between neighbouring subsets (*ie.* placing younger crops in close proximity to other younger crops), as in Figure 7.8 a), yields a slightly lower value for both E_{mean} and E_{stdev}.

The choice of crop ages in a domain may also influence the values of E_{mean} and E_{stdev}. As may be seen from Table 7.5, at 0% initial infestation after harvesting, a 200 m × 200 m domain containing three crop ages, namely crops of 0, 8 and 16 months old, grouped into three subsets, yields a slightly lower value of E_{mean} compared to a similar domain divided into three subsets containing crops of ages 0, 3 and 12 months. The value of E_{stdev}, however, is significantly lower. This is consistent with the results reported in Table 7.3, since if crop ages are not uniformly spread over the sugarcane cycle, with two crop ages close to one another, the results will closely resemble that of a simulation with only two crop ages. It is expected that the values of E_{mean} and E_{stdev} should lie somewhere between that of a domain with only two crop ages, and a domain with three crop ages uniformly spread over the sugarcane cycle.

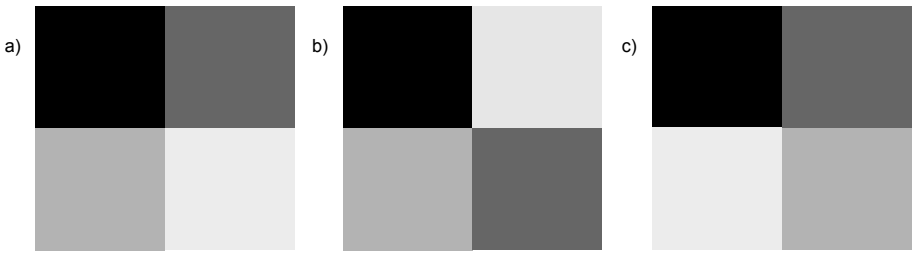


FIGURE 7.8: *A four-hectare 200 m × 200 m domain divided into four subsets, with four crop ages present. a) Variation 1. Top left colour represents 0 month old cane, top right colour represents 6 month old cane, bottom left colour represents 12 month old cane and bottom right colour represents 18 month old cane. b) Variation 2. c) Variation 3. The colour codings in b) and c) have the same meanings as in a).*

	Initial infestation					
	0%		1%		100%	
Variation	Average	Standard deviation	Average	Standard deviation	Average	Standard deviation
1	11.64	6.61	14.67	8.14	20.06	10.65
2	11.63	6.65	15.34	8.59	20.07	10.66
3	11.63	6.63	14.72	8.27	20.06	10.66

TABLE 7.4: *The values of E_{mean} and E_{stdev} for a four-hectare domain divided into four subsets, with different age arrangements, as illustrated in Figure 7.8.*

7.5 Practical recommendations

The results reported in §7.4 may be summarised as follows:

1. *Group same aged crop together.* From the simulation results in §7.4, it is clear that a domain in which the same aged crops are grouped together yields lower average infestation levels over time. Also, the standard deviation is minimised, and so the risk of high infestation periods is minimised.

2. *Minimise the length of boundaries shared between differently aged cane fields.* It is expected that most of the infestation occurring in a field is as a result of cross-infestation from neighbouring fields. If the lengths of boundaries shared between differently aged subsets are minimised, cross-infestation will be minimised, and so too the average infestation level

	Initial infestation					
	0%		1%		100%	
Crop age (in months)	Average	Standard deviation	Average	Standard deviation	Average	Standard deviation
$0, 8, 16$	10.46	6.43	14.28	8.64	19.71	10.92
$0, 4, 18$	11.42	9.04	14.85	11.41	20.40	13.74

TABLE 7.5: *The values of E_{mean} and E_{stdev} for a four-hectare domain divided into three subsets with a different choice of crop ages.*

of the domain.

3. *Minimise the difference in area between differently aged cane fields.* A domain containing different subsets of equal surface area, results in a lower standard deviation from the average infestation level. A lower standard deviation ensures that the peaks in periods of high infestation are minimised.

4. *Choose the number of subsets such that the surface area of the differently aged fields are large enough.* A small domain may not be optimally divided if there are too many different crop ages present in the domain, since the different subsets will then each have small surface area. The surface area of subsets should be at least 1 ha, as may be seen from the results of a four-hectare domain divided into four subsets of 1 ha each, versus a domain of 4 hectares divided into three subsets of 1.33 ha each. If the subsets are too small, average infestation levels may increase.

5. *Choose crop ages uniformly spread across the sugarcane cycle.* A domain with crop ages uniformly spread over the sugarcane cycle results in a lower standard deviation from the average infestation level compared to a domain for which the opposite is true.

6. *Minimise the difference in crop age between neighbouring subsets.* A domain in which subsets with older crop are arranged in between subsets of much younger crop may yield higher infestation levels. It is therefore better to arrange subsets in such a way that the difference in crop age between neighbouring subsets is minimised.

The results reported in §7.4 may be dependent on the assumption of a constant diffusion coefficient. A further recommendation includes the investigation of average infestation levels in differently structured heterogeneous domains with variable diffusion coefficients.

7.6 Implications for SIT

Three possible initial infestations were assumed in this chapter, namely 0%, 1% and 100% initial infestations. If infestation occurs in the form of pure diffusion from neighbouring subsets, the choice of 0% initial infestation is appropriate for a newly planted or harvested subset. SIT may then be applied only along the boundaries of the different subsets, thus forming a 'barrier' which prevents cross-infestation between differently aged subsets. In contrast to results from Chapter 5, the size of the subset (distance between release lanes) will make no difference in the success of the SIT applied, since sterile moths only need to prevent cross-infestation between neighbouring subsets. The release ratio (the number of sterile moths released for every fertile moth in a subset) required would be less than the release ratio required for the case of an initial infestation of 100% of a newly planted/harvested area.

A 0% initial infestation is, however, unlikely in the sense that not all *E. saccharina* are likely to be removed during harvest time, or that some of the seed cane may not be clean, or that some moths do not only spread gradually (a small fraction of *E. saccharina* moths may be far flyers infesting neighbouring areas within-field and not only along the edges as with a pure diffusive process). An initial infestation between 0% and 100% may therefore be more appropriate to assume, given all the possibilities listed which may result in within-field infestation. The 'SIT' barrier will not be sufficient if within-field infestation occurs. Also, the SIT 'barrier' between the differently aged subsets will not be sufficient in preventing cross-infestation if moths disperse mainly as a result of searching for possible oviposition sites, instead of searching for possible

mates. Females may then fly through the SIT 'barrier' into a neighbouring subset, resulting in within-field infestation. Sterile insects will have to be released along the edges of the fields within the subsets instead of just along the boundaries ('barrier') between different subsets. The results of Chapter 5 are applicable when assuming a low level of infestation across 100% of the subset. However, if smaller clusters of initial infestation occur, the release ratio required for suppression will be somewhere between the 'barrier' ratio and the 100% ratio.

7.7 Chapter summary

The effects of a diversified sugarcane habitat on average *E. saccharina* infestation levels in a domain were considered in this chapter. Various ways in which the cost-efficiency of SIT applied on *E. saccharina* in sugarcane were described in §7.1. In §7.2, the optimal diversification of sugarcane habitats were considered as an option for minimising *E. saccharina* infestation, and as a further consequence, the cost-efficiency of SIT. Simulations of the reaction-diffusion model (with constant diffusion coefficients), described in Chapter 5, were performed on various heterogeneous domains (in terms of crop age) and the results of these simulations were reported in §7.4. A summary of the results, in the form of six practical recommendations for sugarcane habitat diversification, were given in §7.5. The implications of an optimally diversified sugarcane domain on SIT were finally described in §7.6.

CHAPTER 8

Conclusion

Contents

"Begin thus from the first act, and proceed; and, in conclusion, at the ill which thou hast done, be troubled, and rejoice for the good."

— Pythagoras of Samos

This chapter contains a brief summary of the work presented in this dissertation together with an overview of the contributions of the dissertation with respect to the SIT research currently conducted on the control of *E. saccharina*. The chapter closes with a number of proposals for future work to further this study.

8.1 Dissertation summary

In the introduction to this dissertation, a short review of the sugarcane industry in South Africa was given together with a brief history of *E. saccharina* infestation in South Africa. The importance of the sugarcane industry to employment and the national economy was emphasised together with the fact that *E. saccharina* infestation is causing major financial losses to the industry. The chapter included a summary of research recently and currently performed at SASRI on means of effectively managing the pest, with the most recent research programme being SIT. The scope of and objectives pursued in this dissertation were also described in Chapter 1.

In Chapter 2, a biological background was provided with respect to sugarcane farming in South Africa, the pest species *E. saccharina* and SIT (in fulfilment of Dissertation Objective I, as stated in §1.3). Biological background information given on the lepidopteran species *E. saccharina* included the description of the insect's lifecycle, its population dynamics in sugarcane, mating behaviour and movement patterns. Current strategies for controlling infestation levels in sugarcane were also reviewed, including early harvesting, pre-trashing, the use of resistant cane varieties and habitat management. The chapter closed with an overview of SIT in general

and also specifically with respect to lepidopteran species. The chapter provided the necessary biological foundation in order to understand the research assumptions made during model construction in subsequent chapters.

A review of the mathematical modelling work related to *E. saccharina* population growth in sugarcane was given in Chapter 3 (in partial fulfilment of Dissertation Objective II). General mathematical models of sterile insect releases were discussed, which included a discussion on models for sterile releases within insect populations with two life stages, as in the case of *E. saccharina* (in partial fulfilment of Dissertation Objective II). The parameters to take into consideration when modelling SIT were emphasized, and include competitiveness, residual fertility, migration and the effect of multiple matings on mating probabilities. Finally, a general discussion on reaction-diffusion theory, which is the main modelling approach adopted in this dissertation, was given — deriving the appropriate system of partial differential equations and describing its application in population biology together with a numerical method (called the *finite-difference method*) which may be used to approximate solutions (in final fulfilment of Dissertation Objective II).

Under the assumption that individual organisms encounter one another in proportion to their average abundance across space, a discrete and deterministic temporal model, which comprises a system of difference equations representing the change in population growth and interaction with sterile released moths over time for each of the four life stages of the insect, was derived in Chapter 4. The assumptions made in order to derive the model were stated, and a detailed description was given of the parameters considered (in fulfilment of Dissertation Objective III). The *E. saccharina* growth, stage-specific maturation and mortality parameters, with the exception of the density-dependent parameter, were all adopted from previous modelling work on *E. saccharina* population growth in sugarcane as described in Chapter 3 (in partial fulfilment of Dissertation Objective III (a)). The density-dependent parameter was introduced in this dissertation in order to incorporate, in very simplified terms, the interaction between *E. saccharina* infestation and sugarcane age. The SIT parameters, namely c_m, c_s, c_f, β and q, were estimated from previous and concurrent entomological research (in partial fulfilment of Dissertation Objective III (a)). Derivations of the fertilization probabilities (in final fulfilment of Dissertation Objective III (a)), γ and ρ, were given, which, in contrast with previous SIT models where only the male mating probabilities were considered, include both the probability of mating with a certain type of male (fertile or sterile) and mating with a certain type of female. In order to determine the economic viability of different sterile release strategies, model output parameters were defined which include the cost of a release strategy, the crop damage index and the increase in revenue expected from different strategies (in fulfilment of Dissertation Objective VI). The model output was validated by means of limited data sets obtained from the Sezela mill and the pilot site, and also by means of sterile release ratios required in previous SIT projects (in fulfilment of Dissertation Objective III (d)). The optimal release frequency and ratio for an assumed parameter set was obtained by means of numerical simulation (in partial fulfilment of Dissertation Objective V)— the optimal release frequency in terms of profit being weekly releases. Sensitivity analyses (in fulfilment of Dissertation Objective III (c)) revealed that δ is very sensitive around η_{opt}; therefore a better strategy (in terms of both profit and risk) may be chosen where $\eta > \eta_{opt}$, but still within the profit range of η. Sensitivity analyses also revealed that the model output was more sensitive to changes in c_m than to changes in c_f, indicating that males have a more significant impact on suppression than females — it may therefore be advisable only to release males. Releases commenced at a crop age of between 0 and 5 months was found to be better in terms of both profit and damage levels, although a profit may still be obtained when releases commence at other crop ages less than 12 months.

The temporal model of Chapter 4 was extended in Chapter 5 to a spatially explicit model (a discretized reaction-diffusion system with zero-flux Neumann boundary conditions) in order to describe *E. saccharina* growth and dispersal in a spatially and temporally variable environment and to investigate the effect of dispersal on SIT (in fulfilment of Dissertation Objective IV). Although constant diffusion coefficients were assumed in simulations, the spatio-temporal model was derived generally for variable diffusion coefficients. The numerical solution to the system of partial differential equations was approximated by means of the *finite difference method*, whereby the optimal release method and distribution were obtained for suppression at a minimum cost (in final fulfilment of Dissertation Objective V). Numerical results indicated that twice-a-week releases was the best option in terms of risk, whereas weekly releases was the best option in terms of SIT profit — suppression may be achieved at smaller release ratios and larger distances between release lanes when releases are twice a week, but SIT costs are then much higher. The maximum distance between ATV release lanes at which suppression is possible was estimated to range between 15 m and 30 m, depending on the release method, frequency and dispersal rate. In the case of aerial releases for the assumed range of the dispersal rates, it was established from simulations that, if the position of the release lanes remain constant over time, moths should spread between 90 and 100 metres in the air before reaching the sugarcane canopy in order to achieve suppression at release ratios which are economically viable. Non-stationary aerial release distributions performed better than stationary aerial release distributions - suppression was obtained with moths spreading between 10 metres and 50 metres. Results also indicated that, in terms of SIT profit, the cost per sterile insect should satisfy $\kappa_r < 0.1$ in order to obtain an economically viable strategy (in final fulfilment of Dissertation Objective VI). Aerial releases, with currently available aircraft were not considered viable in terms of cost. However, if application costs for UAVs are significantly lower, aerial releases may be considered. The model results were also validated by means of data obtained from similar SIT projects, and compare well with release ratios and distances adopted in other SIT projects in South Africa.

The practical workability of the spatio-temporal model was demonstrated in Chapter 6 by developing a user-friendly simulation tool for *E. saccharina* population dynamics under the influence of SIT (in fulfilment of Dissertation Objective VII). In §6.1, a description of the simulation tool was given, along with ideas for future expansion. In §6.3, a detailed description of the tool's graphical user interface was given. The input values expected in order to perform simulations were described, as well as the output values which are available after simulations. An example simulation was provided in §6.4, with the domain representing a pilot site near Eston, Kwazulu Natal. The results of simulations performed on this realistic sugarcane domain were given in §6.4.2, with resulting recommendations in §6.4.3 (in fulfilment of Dissertation Objective VIII). The purpose of this chapter was to introduce a basic platform from which different release strategies may be investigated with respect to various spatial domains. Ideas for future expansion of the simulation tool were also given — it may be extended to a DSS for use in an AW-IPM. The difficulties encountered in applying the model to a real-life scenario were touched upon, as well as the assumptions made to overcome these difficulties.

Simulations of the reaction-diffusion model (with constant diffusion coefficients), described in Chapter 5, were performed on various heterogeneous domains (in terms of crop age) in Chapter 7 to investigate the effects of a diversified sugarcane habitat on average *E. saccharina* infestation levels (in partial fulfilment of Dissertation Objective VIII). An optimal diversification of sugarcane habitats was considered as an option for minimising *E. saccharina* infestation, and as a further consequence, improving the cost-efficiency of SIT. Simulation results were reported in §7.4. A summary of the results, in the form of six practical recommendations for sugarcane

habitat diversification, were given in §7.5. The results reported depend on the assumption of constant diffusion coefficients. A more realistic approach may include the assumption of sugarcane age-dependent diffusion coefficients. The implications of an optimally diversified sugarcane domain on SIT were finally described in §7.6.

8.2 The main contributions of this dissertation

The main contributions of this dissertation are outlined in this section within the context of SIT research currently conducted in South Africa.

Contribution 1 *A reaction-diffusion model for a species with four life stages in a spatially and temporally variable environment under the influence of SIT.*

A reaction-diffusion model was applied to *E. saccharina* growth and dispersal with sterile releases in a spatially and temporally variable environment. Most of the published models of sterile insect releases are theoretical, with very few examples in the literature on spatio-temporal SIT models applied to a specific species with more than one life stage and where F1-sterility is applicable. More specifically, no examples exist in the literature of an SIT model for *E. saccharina*. Also, previous mathematical formulations of *E. saccharina* growth and dispersal only considered the spatial movement of *E. saccharina* in simplified terms by means of simulation where a constant dispersal rate was assumed between neighbouring fields. No mathematical models have previously been derived by which the spatial movement of *E. saccharina* may be described across the entire domain (within-field as well as between-field dynamics). The reaction-diffusion system adopted in this dissertation was discretized by means of the *finite difference method* in order to approximate solutions to the system of partial differential equations. A method for solving the resulting Neumann boundary value problem with variable diffusion coefficients on a discretized domain was also developed.

Contribution 2 *Mathematical expressions for estimating mating and fertilization probabilities for multiple matings if fully sterile females and partially sterile males are released.*

Mating and fertilization probabilities may be found in SIT literature for the cases where sterile or partially sterile males are released. However, the author could not find any derivation of mating and fertilization probabilities in the SIT literature for the case where fully sterile females and partially sterile males are released and therefore the relationships derived in §4.4.1 are deemed to be newly proposed in this dissertation. As a result, the contribution of both sterile females and males towards suppression could be investigated.

Contribution 3 *Practical recommendations for SIT in sugarcane.*

Numerical and sensitivity analyses resulted in easily interpretable results and practical recommendations for the application of SIT in *E. saccharina* populations in sugarcane, which include suggestions as to male-only releases, the best release frequencies and ratios in terms of profit and risk, the cost per sterile insect for SIT to be economically viable, best distributions of release sites and release ratios whereby suppression may be obtained for the different release distributions.

Contribution 4 *An investigation into the effectiveness of different sterile release methods in the sugarcane context.*

Formulation of the reaction-diffusion model made it possible to investigate different sterile release distributions on a spatial domain, and as a result provided practical recommendations for distributions whereby suppression may be obtained. The current release method adopted by SIT companies in South Africa include ATV releases by hand or with a mechanical device. Aerial releases from currently available aircraft are considered too expensive. Within the sugarcane context, ATV releases are only possible along the paths between the sugarcane fields, and determining whether ATV releases are a viable method of release whereby suppression may be obtained in a given field layout is important — commencing SIT in sugarcane should otherwise be postponed until a less expensive means of aerial releases (such as UAVs) becomes available.

Contribution 5 *A simulation tool for predicting economically viable release strategies whereby suppression may be obtained in differently shaped spatial domains.*

A simulation tool was developed for simulating *E. saccharina* infestation in sugarcane under the influence of SIT releases. The development of the simulation tool, as described in Chapter 6, provides the reader with a deeper understanding as to what is involved in applying mathematical models, such as those developed in this dissertation. The model output parameters, as defined in §4.5 and §5.5, provide a means by which the economic viability of different release strategies in sugarcane may be investigated. MATLAB code was developed by which GIS shapefiles of different spatial domains (release sites, each with a unique field layout) may be transformed into matrix data structures. Together with the spatio-temporal model implementation in MATLAB, it provides a means by which the spatio-temporal model may be simulated and analysed over differently shaped spatial domains, thereby making it possible to predict economically viable release strategies whereby suppression may be achieved in the given domain.

8.3 Possible future work

As with most research projects, time does not always allow for the pursuit of all the ideas conceived during the period of study. The work presented in this dissertation is by no means complete: better techniques, assumptions and approaches, given more time, may have been adopted resulting in models of higher quality. This section therefore contains suggestions with respect to possible future research (in fulfilment of Dissertation Objective VIII), from both entomological and mathematical points of view.

8.3.1 Recommendations for future entomological research

Most of the parameters employed in the models in this dissertation were taken from previous studies on *E. saccharina* growth and infestation in sugarcane. Sterile insect-specific parameters were also obtained from previous and current studies on the effects of radiation on the insect, although some values have not yet been confirmed by means of sufficient quantities of data (for example, the parameters c_f, c_m and c_s). However, all of the growth and sterile insect-specific parameters are within an accepted range of accuracy. Parameters relating to the movement patterns of *E. saccharina* have not yet been estimated experimentally; more information in this respect is required in order to incorporate further biological realism into the models contained

in this dissertation. The following recommendations are made with respect to possible future entomological research on *E. saccharina*.

Proposal 1 *Investigate the spatial working memory of the E. saccharina moths.*

The use of a pure diffusion process in the model described in §5.3 with constant diffusion coefficients is based on the assumption that individual moths follow a pure random walk. As mentioned in §5.2, this assumption is only realistic if individual moths have no long-term memory or large-scale information of the landscape [79]. Recent research has indicated that insects exhibit decision-making processes in their spatial movement patterns, and therefore possess some measure of spatial working memory [43, 76, 91]. In order to incorporate a higher level of biological realism into the model, more information is required with respect to the spatial movement patterns of *E. saccharina* moths, and how it effects dispersal rates for different cane varieties and cane ages.

Proposal 2 *Measure the dispersal rate of E. saccharina moths.*

The model described in Chapter 5 assumes a diffusion coefficient (dispersal rate) which ranges between 0.005 and 0.03. This range for the diffusion coefficient was obtained from a study by Berry *et al.* [16] in which the observation was made that *E. saccharina* was able to colonize most of a 0.65 ha field. The study, however, did not explicitly measure dispersal rates over time, and therefore the assumed values for the diffusion coefficient used in this dissertation are only rough estimates. More information is required on how fast moths disperse over some spatial domain in order to be able to measure required release ratios more accurately.

8.3.2 Possible future modelling and simulation work

The mathematical models presented in this dissertation are based on certain assumptions in order to simplify representation of the real world processes. The models put forward in Chapters 4 and 5 should therefore by no means be interpreted as "correct" representations of SIT applied to *E. saccharina* in the real world, but rather as an approximation (in accordance with the assumptions made). By changing some of the assumptions made, better approximations may be obtained. Possible future modelling work may include the following proposals.

Proposal 3 *Perform simulations with variable diffusion coefficients.*

As mentioned in §8.3.1, recent research has indicated that some insects exhibit decision-making processes in their spatial movement patterns, and therefore possess spatial working memory to some extent [43, 76, 91]. If individual *E. saccharina* moths display spatial working memory, their movements cannot be described by a pure random walk and adjustments have to be made to the diffusion model. In order to incorporate a higher level of biological realism into the model, one possible adjustment might be to assume spatial heterogeneity not only in the mortality of *E. saccharina* larvae, but also in the movement patterns of *E. saccharina* moths. A variation in the diffusion coefficients according to the habitat type may be assumed if *E. saccharina* moths exhibit an hierarchical choice with respect to cane variety and cane age [78, 79]. The diffusion coefficient may therefore be assumed to depend upon the age (time) and variety of the sugarcane at position $\underline{\xi} = [\xi_1, \xi_2]^T$. Another possible adjustment may be to assume that the diffusion

coefficient also depends upon the temperature τ. During cold winter months, *E. saccharina* moths appear to be less active [35], which would result in a smaller diffusion coefficient than during the summer months. A further possible study may include the effect of density-dependent diffusion coefficients — for example, it may be assumed that for small densities moths may be more inclined toward concentrating (negative diffusion coefficients), whereas for larger densities moths may be more inclined toward spreading (positive diffusion coefficients). The model described in Chapter 5 was derived in such a way that variable diffusion coefficients easily be incorporated into the model; therefore, no adjustments to the model structure is necessary.

Proposal 4 *Investigate infestation levels on differently structured heterogeneous domains with variable diffusion coefficients*

The results presented in Chapter 7 are subject to the assumption of constant diffusion coefficients, which may be an unrealistic assumption. The results obtained indicate that same-aged fields should all be grouped together into larger subsets in some optimal arrangement in order to minimise average infestation levels across the domain. However, *E. saccharina* infestation is more inclined to spread faster in older sugarcane than in younger cane. Dispersal may therefore be sugarcane age-dependent. A logistic function may be an appropriate function for describing sugarcane age-dependent diffusion. This will cause the dispersal to be limited in younger sugarcane, gradually increasing with the sugarcane canopy, and reaching a maximum at a certain sugarcane age. In this case, infestation levels may be decreased if same-aged fields are not grouped together, but rather exhibiting more diversified spatial patterns (such as a checkerboard pattern, where fields containing older sugarcane are surrounded by fields containing younger sugarcane).

Proposal 5 *Incorporate stochasticity into the models.*

The models put forward in Chapters 4 and 5 are deterministic models. Although it is accepted that deterministic models may yield reasonable approximations of stochastic events such as birth and death processes, stochastic models are still considered better approximations of these processes, and may indicate how, for example, weather conditions and dispersal patterns influence these processes. Maturation and mortality rates of *E. saccharina* are temperature-dependent [7, 52, 111]. However, the temperatures adopted in this dissertation was estimated by means of the average temperatures for each month. The temperature on a specific day may rather be estimated by means of a probability distribution of temperature for each month. In addition, the growth, mortality and maturation parameters have all been obtained from average rates calculated as a result of laboratory experiments. Each parameter, however, has its own probability range which may also be incorporated into the models by the introduction of stochastic terms.

Proposal 6 *Research ways in which the within-field distribution of E. saccharina may be modelled more accurately.*

Although *E. saccharina* infestation was spread-out over most of the field at the end of the crop cycle in the study by Berry *et al.* [16], the within-field distribution patterns of *E. saccharina* seemed to be clustered to some extent, rather than exhibiting an even spread as in the case of a pure diffusion process with positive, constant diffusion coefficients. If initial populations are distributed randomly across space, and the diffusion coefficient is small enough, spreading

is limited, although it still does not produce the within-field distribution patterns observed by Berry *et al.* [16].

The effect of negative diffusion coefficients in the spatio-temporal model was tested in order to see whether it may produce the desired concentration effect. For initial infestation in $\mathcal{S}_p$ equal to $1e/100s$ and initial infestation equal to $0.9e/100s$ in $\mathcal{S}_{p'}$, gradual concentrating of *E. saccharina* did occur, with concentration occuring faster for larger values of $|d(\underline{x}, t)|$ (see Figure 8.1). If $|d(\underline{x}, t)|$ is too large, however, the reaction terms in the model yield lower values than the diffusion terms, which result in *E. saccharina* population densities in neighbouring nodes tending to negative and positive infinity, respectively, after a certain time t. This behaviour is expected for a model with negative diffusion coefficients as differences between neighbouring nodes become all the more pronounced as time increases. From a biological perspective, however, population densities may never become negative and diffusion coefficients need to be chosen appropriately. The range for the diffusion coefficient assumed in this dissertation is small $(0.01 \leq d(\underline{x}, t) \leq 0.025)$ and within the bounds for which the finite-difference approximation converge [96]. The instability caused by the negative coefficients used in the above example is an illustration that the finite-difference approximation do not converge for all values of $d(\underline{x}, t)$. A more thorough study on the range of values of $d(\underline{x}, t)$, for which the approximation converge, is required before adding negative coefficients to the range used in the spatio-temporal model described in Chapter 5.

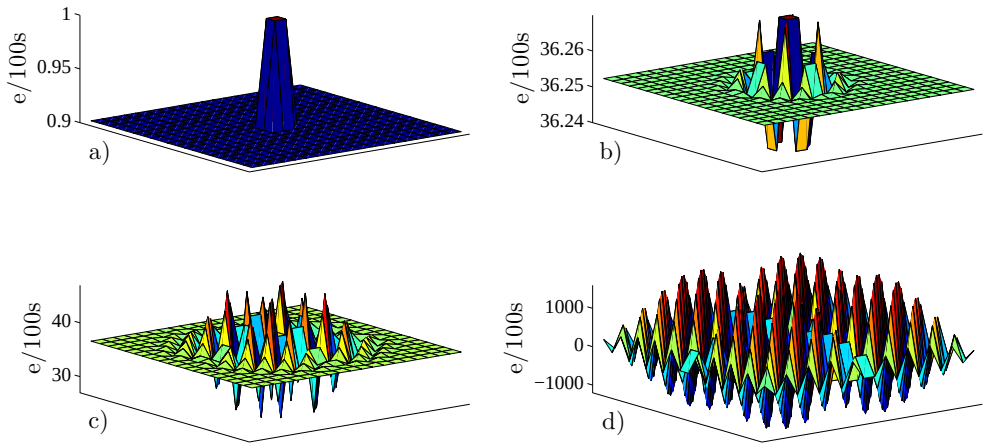


FIGURE 8.1: *Moth population densities for different diffusion coefficients. (a) Moth population density at the beginning of the crop cycle, (b) moth population density at the end of the crop cycle with* $d(x_1, x_2) = -0.005$*, (c) moth population density at the end of the crop cycle with* $d(x_1, x_2) = -0.01$*, (d) moth population density at the end of the crop cycle with* $d(x_1, x_2) = -0.015$*.*

Proposal 7 *Incorporate various types of control measures into the spatio-temporal model simultaneously.*

SIT is typically considered as part of an AW-IPM in which the use of pesticides, biological control, habitat management and SIT are combined in the control against *E. saccharina* infestation. In order to estimate the release ratios necessary for a succesful AW-IPM, the spatio-temporal model has to incorporate all types of control measures. Horton [52] investigated the effects of biological control on infestation levels. This dissertation concentrated on the effect of SIT on infestation levels. No mathematical study has yet been undertaken on the effects of habitat management on infestation levels, and more specifically the use of push and pull plants. A

possible way of modelling the effects of push and pull plants may be to adjust the boundary conditions. The spatio-temporal model of Chapter 5 assumes zero-flux Neumann boundary conditions. This may be adjusted to non-zero flux Neumann boundary conditions in the case of pull plants.

Proposal 8 *Incorporate longer range dispersal across fragmented landscapes into the models.*

The spatio-temporal model described in Chapter 5 assumes local dispersal of both males and females within a bounded continuous spatial domain. However, no dispersal between different spatial domains was considered (fragmented landscape). Although it is reasonable to assume local dispersal of both males and females, some individuals may disperse over considerable distances (up to 200 m) with the female, being larger and stronger than the male, the more likely to disperse [5, 8, 25] across different domains. The *E. saccharina* infestation problem therefore actually occurs on a larger scale (across numerous farms), and adjustments to the model are therefore necessary to incorporate area-wide control on fragmented landscapes [121].

Proposal 9 *Find a method for estimating the dispersal proportions of fertile, inherited and released sterile moths.*

In the models described in §4.3 and §5.3, the moth populations were subdivided into three populations, namely fertile, inherited sterile and released sterile moths. Dispersal in each subpopulation was assumed to occur according to the average gradient of each subpopulation. Dispersal in actual fact occurs as a result of the combined moth population reacting according to the average gradient of the total combined moth population. In order to obtain the number of dispersing moths at position $\underline{\xi}$ which are fertile, inherited sterile and released sterile moths, respectively, the total dispersing moths at position $\underline{\xi}$ has to be divided into the three groups in such a way that $\sum_{\underline{x}} \nabla \mathbf{D}(\underline{x}) \cdot \nabla \underline{\mathcal{E}}(\underline{x}, t) + \mathbf{D}(\underline{x}) \nabla^2 \underline{\mathcal{E}}(\underline{x}, t) = 0$ for all three moth populations and also in relation to the proportions of fertile, inherited sterile and released sterile moths at position $\underline{x}$. A number of methods for computing the dispersal proportions were attempted which resulted in either $\sum_{\underline{x}} \nabla \mathbf{D}(\underline{x}) \cdot \nabla \underline{\mathcal{E}}(\underline{x}, t) + \mathbf{D}(\underline{x}) \nabla^2 \underline{\mathcal{E}}(\underline{x}, t) \neq 0$ with dispersing moths in relation to the proportions of fertile, inherited sterile and released sterile moths at position $\underline{x}$, or $\sum_{\underline{x}} \nabla \mathbf{D}(\underline{x}) \cdot \nabla \underline{\mathcal{E}}(\underline{x}, t) + \mathbf{D}(\underline{x}) \nabla^2 \underline{\mathcal{E}}(\underline{x}, t) = 0$ with dispersing moths not in relation to the proportions of fertile, inherited sterile and released sterile moths at position $\underline{x}$. One common problem which occurred was when a moth subpopulation was not present at position $\underline{x}$ during a specific timestep — after migration the subpopulation assumed negative values at position $\underline{x}$, which is not biologically feasible (and also not according to the proportion of the subpopulation at position $\underline{x}$). One important feature of all the methods considered was that the error during each timestep increased with time, whereas the error of the method adopted in the model described in §5.3 decreases with time.

Proposal 10 *Obtain sugarcane growth parameters from the CANEGRO or CaneSim models.*

In this dissertation, interaction between *E. saccharina* population growth and sugarcane growth was incorporated by adjusting the values of y and z in (4.38). However, it is not possible to incorporate all sugarcane growth factors and their impact on *E. saccharina* by only adjusting the values of y and z. A useful addition to the model may be to obtain sugarcane growth parameters from the CANEGRO model [18], similar to the CANEGRO addition used by Horton [52], and to incorporate the possible change in *E. saccharina* infestation parameters accordingly. Another model that may be incorporated to obtain sugarcane growth parameters, is the CaneSim model [94, 95].

Proposal 11 *Include the effect of E. saccharina damage on fibre levels in sugarcane.*

Stalks bored by *E. saccharina* typically have a lower sucrose content, and a higher fibre level [112]. Only lower sucrose levels was accounted for in this dissertation, with little data available on the relationship between fibre levels and *E. saccharina* damage. The RV values estimated in this dissertation, as described in §4.5 and §5.5, are therefore slightly overestimated. The increase in revenue as a result of SIT may therefore be higher than estimated, and therefore a slightly higher SIT profit may be expected.

Proposal 12 *Extend the SIT simulation tool put forward in Chapter 6 to incorporate some of the above mentioned proposals.*

The SIT simulation tool developed in Chapter 6, may be further refined to accommodate variable diffusion coefficients, output from more complicated sugarcane models, and other control measures. Furthermore, the SIT simulation tool may be extended to function as a DSS within an AW-IPM.

Proposal 13 *Approximate solutions by adopting the finite element methodological approach.*

The finite element method is an alternative modelling approach towards approximating solutions in the real-world system (5.6). Although the finite difference method is easier to implement, the finite element method is able to accommodate complicated geometries (as in the case of sugarcane fields) much better than the finite difference method [122].

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APPENDIX A

Contents of the accompanying compact disc

Included with this dissertation is a compact disc containing the MATLAB implementations of the models described in Chapters 4, 5, as well as the simulation tool of Chapter 6. All the MATLAB files are unprotected and may be opened in the MATLAB editor for modification. This appendix contains a brief description of the contents of the compact disc. There are four directories on the compact disc, namely *Dissertation*, *Mean-field model*, *Spatio-temporal model* and *SIT Simulation Tool*. The contents of these folders are described below.

Dissertation. This folder contains an electronic copy of the dissertation in ".pdf" format.

Mean-field model. This folder contains the implementation of the mean-field model as MATLAB script files (".m" format). The main file from which simulations may be initiated is called "Eldana.m". This file contains the *E.saccharina* growth and SIT parameters which were used in simulations, and of which the values may be altered in accordance with the specific scenario considered.

Spatio-temporal model. This folder contains the implementation of the spatio-temporal model as MATLAB script files (".m" format). The main file from which simulations may be initiated is called "Eldana_main.m". This file contains the *E.saccharina* growth and SIT parameters, as well as the diffusion and domain-specific parameters. The values of these parameters may be altered in accordance with the specific scenario considered.

Simulation tool. This folder contains the implementation of the simulation tool described in Chapter 6, with both the mean-field model and the spatio-temporal model applied to various spatial domains and a corresponding graphical user interface, as MATLAB script files (".m" format). The main file containing the graphical user interface is called "Eldana_GUI.fig". This file may be opened through the graphical user interface development environment (GUIDE) of MATLAB by selecting "Graphical User Interface" under the "New" menu on the "Home" tab. The graphical user interface is invoked by selecting the "Run" command under the "Tools" menu or by clicking the green "play" button in the quick menu of GUIDE. Simulations may be initiated by clicking the green button in the top right corner. The sugarcane, SIT and Eldana parameters as well as the simulation time may be configured on the graphical user interface before each simulation run. The simulation tool was developed to obtain the sugarcane field layout information from a shapefile containing any number of features. Each of these features should be of type "polygon", consist of a set of x and y coordinate pairs (defining the shape of the field) and have a caption comprising the field label (e.g. "3C") and the field age in months (e.g.

"6mnths"). The information is obtained from the shapefile using the MATLAB commands "shapeinfo" and "shaperead".

The code generates a number of output parameters, of which the most important are:

a) *harvLargeLarvae:* The spatial distribution of larvae at harvest times.

b) *aveLargeLarvae:* The average infestation per field per day.

c) *averageLargeLarvae:* The average infestation over the domain per day.

d) *harvPercentDamage:* The spatial distribution of percentage damage at harvest times.

e) *harvTotalCost:* The total SIT cost for the domain over the entire simulation period.

f) *aveHarvestRevenue:* The average revenue at harvest time for each field.

g) *totalRevenue:* The total revenue for the domain over the entire simulation period.